SITE FIDELITY:

DEFINITION, MEASUREMENT AND IMPLICATIONS FOR POPULATION STRUCTURE USING MARK-RECAPTURE, GENETIC, AND COMPARATIVE DATA IN THE HOODED, RED-BREASTED, AND COMMON MERGANSER

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

John Maunsel Pearce, M.S.

Fairbanks, Alaska

December 2008

SITE FIDELITY:

DEFINITION, MEASUREMENT AND IMPLICATIONS FOR POPULATION STRUCTURE USING MARK-RECAPTURE, GENETIC, AND COMPARATIVE DATA IN HOODED, RED-BREASTED, AND COMMON MERGANSERS

By

John Maunsel Pearce

RECOMMENDED:

Dr. Paul Flint

Dr. Matt Olson

Dr. Kevin Winker

Dr. Mark Lindberg, Advisory Committee Co-Chair

Dr. Kevin McCracken, Advisory Committee Co-Chair

Richard Boone

Dr. Rich Boone, Chair,
Department of Biology and Wildlife

APPROVED:

Dr. Joan Braddock, Dean,
College of Natural Science and Mathematics

Lawrence K Duffy

Dr. Lawrence Duffy, Dean of the Graduate School

Nov 21, 2008

Date

Abstract

For species that return each year to the same breeding or nonbreeding area, subsequent biological assumptions have included population genetic structure, demographic independence, and possible irreversible extirpation of a site-faithful group due to low immigration. Little is known about patterns of site fidelity, population structure, and migratory patterns of the three species of mergansers that breed and winter in North America: the Hooded Merganser (*Lophodytes cucullatus*), the Red-breasted Merganser (*Mergus serrator*) and Common Merganser (*M. merganser*). The primary objective of this study was not only to infer general levels of site fidelity with different data types (mark-recapture and genetic), but also to examine the inherent assumptions of site fidelity studies and biases of various methods, such as genetic and mark-recapture. A secondary objective was to provide additional information on the natural history of merganser species in North America.

Genetic characteristics of all three merganser species across North America represented a range of subdivision from panmixia to well-differentiated, likely resulting from species-specific nesting ecologies, life history traits, and responses to historical climate change. These genetic patterns were not always consistent with expectations from other data sets, such as mark-recapture estimates of nest site fidelity by adult female Hooded Mergansers. The main conclusions of this study are threefold: (1) the definition and implications of site fidelity must be carefully considered, (2) the assessment of site fidelity is best undertaken with multiple and independent markers, and (3) the three merganser species in North America offer a wide range of dispersal

and migratory patterns which demonstrate the importance of adequately assessing site fidelity and its influence on population structure during both breeding and nonbreeding periods.

Table of Contents

List of Figures

Page

CHAPTER 2.

CHAPTER 3.

CHAPTER 4.

List of Tables

Page

CHAPTER 2.

CHAPTER 3.

CHAPTER 4.

Acknowledgments

At the time of completion of this dissertation, the first two chapters had already been published in *The Condor* and *The Auk*, respectively. Chapters 3 and 4 are formatted for submission to *The Auk* and *The Condor*, respectively. Although this dissertation is single authored, multiple coauthors were involved in each individual manuscript. Therefore, the "we" in each chapter refers to the coauthors listed, but I alone am responsible for any errors in this dissertation and for the general introduction and conclusion sections, which are not included in the published manuscripts.

I will be forever grateful to Dirk Derksen at the U.S. Geological Survey, Alaska Science Center (USGS ASC) for convincing me that a Ph.D. was "in the cards". He offered constant support and enthusiasm for my ideas and research. I also thank my graduate advising committee, Kevin McCracken, Mark Lindberg, Paul Flint, Matt Olson, and Kevin Winker for numerous hallway, office and email conversations and for the many analytical and theoretical issues they asked me to tackle as I worked through data analyses and writing. Sandy Talbot helped to formulate many of the initial ideas for this project. I am very grateful to Peter Blums and Leigh Fredrickson for inviting me to collaborate with them on the analysis of their many years of Hooded Merganser mark-recapture data. Dan Esler and Bruce Dugger offered helpful feedback during the early design stages. Paul Flint, John Reed, Jason Schamber, and Margaret Petersen sweated and froze through several "wild merganser chases" during the first year of the study and I very much appreciate their willingness to help. George and Carolyn Rakos graciously offered us the use of their cabin on the Kenai for some of these initial

expeditions. Tuula Hollmén and Dave Saffine (Alaska SeaLife Center) provided good company during captures in Seward. Todd Eskelin and John Morton of the Kenai National Wildlife Refuge (NWR) were also especially helpful during the first year of captures. Special thanks to Sandy Talbot, Kevin Sage, and Judy Gust (all of the USGS ASC) for assistance with laboratory methods and analysis and to Chris Dau (U.S. Fish and Wildlife Service) for his enthusiasm in helping to prepare and archive of all those merganser specimens. The molt migration study (Chapter 4) would never have taken place were it not for Denny Zwiefelhofer (Kodiak NWR) urging me to visit Kodiak in 2004. Tony Erskine (Canadian Wildlife Service), Mick Marquiss (Centre for Ecology and Hydrology, Scotland), and Jo Smith (University of Washington) were great sources of information about mergansers in other parts of the world.

This project would not have been possible without the financial and logistical support of the North American Sea Duck Joint Venture and state and federal agency personnel, including the USGS ASC, the Department of Biology and Wildlife at the University of Alaska, Fairbanks, staff of the Kodiak NWR, Kenai NWR, Izembek NWR, Togiak NWR, Arctic NWR, Yukon Delta NWR, the U.S. Forest Service, and the U.S. Coast Guard. In addition, numerous agencies and individuals contributed time, unpublished banding data and genetic material that made this study possible including: Denny Zwiefelhofer, Nate Maryanski and volunteers (Kodiak NWR), Pete Abraham and Tim Allen (Togiak NWR), Steve Kendall (Arctic NWR), John Morton and Todd Eskelin (Kenai NWR), staff of the U.S. Coast Guard Loran Station Attu and David Sonneborn and Mike Schwitters, staff of the U.S. Forest Service (Chugach and Tongass

Ranger Districts), Jeff Peters and Kevin Omland (University of Maryland), Kevin McCracken, Kevin Winker, Rob Wilson, and Sarah Sonsthagen (University of Alaska, Fairbanks), Paul Padding and Karen Bollinger (U.S. Fish and Wildlife Service), Bill Bower (Ottawa Duck Club), Rosalyn McNeil, and Brigitte Braune (Environment Canada, Wildlife Toxicology Division, Specimen Bank), Chris Davies (Ontario Ministry of Natural Resources), Andy Weik (Maine Department of Inland Fisheries and Wildlife), Ed Robinson (New Hampshire Fish and Game Department), Robert Helm, Mark Edmunds, T. Vidrine, M. Berg, and D. Hayden (Louisiana Department of Wildlife and Fisheries), Lucas Savoy (BioDiversity Research Institute), H. Heusmann (Massachusetts Division of Fisheries and Wildlife), Jim Berdeen and Jeff DiMatteo (Minnesota Department of Natural Resources), Tom Sutter (New York Department of Environmental Conservation), Sharon Birks and Rob Faucette (Burke Museum of Natural History and Culture), Bruce Dugger and Harold Meyer (Oregon State University), Mick Marquiss (Centre for Ecology and Hydrology, Scotland), David Boertmann and Thomas Christensen (National Environmental Research Institute, Denmark), Jo Smith and Julia Parrish (University of Washington), and Roger Strand, Eric Taylor, and Jeff Mason. Devon Berthiaume assisted with initial genotype screening and Dan Ruthrauff helped with the maps. All methods involving live animals were approved by Institional Animal Care and Use Committees at the University of Alaska, Fairbanks (#02-01 and #04-14) and the U.S. Geological Survey (#070707-1).

This work would have been much less enjoyable and rewarding without the friendship and support of fellow grad students, friends, and family. In Fairbanks, I

thank fellow grad students Heather Wilson, Josh Schmidt, Amy Carrol, Travis Booms, David Saffine, Shiway Wang, Hayley Lanier, John Citta, Brant Meixell, and the Feathers on Friday's crowd. For numerous engaging discussions, I thank Dan Esler and Sam Iverson (both of Simon Fraser University), Dan Rizzolo (U.S. Geological Survey), Chris Dau (U.S. Fish and Wildlife Service), Mick Marquiss (Centre for Ecology and Hydrology, Scotland), Naoki Miyabayashi, Diana Wolf, Link Olson, Jeff Peters and Dan Gibson (University of Alaska), and Chris Nicolai (University of Nevada). Tremendous thanks to Dirk Derksen, Mark Lindberg, Kevin McCracken and Paul Flint for monitoring my health, checking my science, and watching out for my future. In Anchorage, all my homies at the USGS ASC are an unending source of support and scientific inspiration. I can't imagine working anywhere else. Although my M.S. graduate committee and student cohorts at the University of Idaho were not directly involved in this project, they established some high standards in me that persist to this day, and I am ever thankful. Besides my committee members, others read drafts of each chapter for clarity and accuracy, including Craig Ely, Dirk Derksen, Josh Schmidt, Leigh Fredrickson, Margaret Petersen, as well as editors and anonymous reviewers of the journals where manuscripts were published. Lastly, none of this would have been possible without the support of my family, both in Utah and Alaska. Elizabeth, Bennett, and Eliot uprooted themselves for our yearlong adventure in Fairbanks so I could be a grad student again. You kept me sane, confident, and appreciated. Whenever you are ready to chase an opportunity, I'll happily be uprooted to support you, wherever that may be.

General Introduction

There are numerous methodological and verbal ways in which to define a group of animals as a "population" (reviewed in Wells and Richmond 1995, Waples and Gaggiotti 2006), and no single method works in all circumstances. However, one method that has been widely applied for inferring the structure and delineation of migratory, vertebrate species is philopatry: the limited dispersal from, or returning to, a birth place for reproduction (Greenwood 1980). In the recent scientific literature, the application of the term "philopatry" and its assumed role in structuring populations genetically, and thus demographically, has widened beyond its original and true definition. The term is now commonly applied to general site faithful behavior of animals to not only breeding areas, but also to non-breeding areas, such as sites used for molting (Iverson et al. 2004), wintering (Robertson and Cooke 1999, Mehl et al. 2004), or stopover during migration (Merom et al. 2000).

Use of the term "philopatry" to describe general site fidelity to both breeding and non-breeding sites of individuals whose natal areas are unknown is problematic and warrants reconsideration. This is because there are substantial genetic and demographic implications of philopatry in its purest and historical sense (i.e., natal philopatry), such as increased relatedness and population differentiation (Greenwood 1980, Avise et al. 1992). Indeed, the historical and theoretical discussions of natal philopatry focus on the behavior of limited dispersal from a birth place, how this promotes inbreeding, why inbreeding might be adaptive, and how a lack of gene flow might promote speciation (Mayr 1963, Shields 1982, Anderson et al. 1992). These

population genetic and demographic implications are potentially misapplied when "philopatry" is used to describe site faithful behavior in general, especially in advance of a complete understanding of dispersal and gene flow among populations. For example, any assessment of site fidelity or migratory connectivity by adults likely includes some immigrant individuals as a result of juvenile dispersal, whereas assessments of natal philopatry include only locally hatched or born individuals. Thus, quantifying migratory connectivity and site fidelity and their implications for population structure must be undertaken cautiously and preferably with multiple, independent data types.

Several assessments of site fidelity have been made for waterfowl species using either mark–recapture or genetic methods (Avise et al. 1992, Lindberg et al. 1998, Blums et al. 2002, Doherty et al. 2002). With mark–recapture methods, estimates of return or homing rates have been used to infer general levels of site fidelity, though these methods are *post-hoc* assessments confounded by mortality and emigration (Doherty et al. 2002). More robust measures of return rates can be obtained through estimation of the fidelity parameter (F), which requires multiple live recaptures of banded individuals on a given study area, as well as the recovery of banded birds outside that study area and throughout the potential range of dispersal and migration (Burnham 1993, Doherty et al. 2002). Similarly, genetic data have been used as indirect measures of site fidelity and dispersal through estimates of genetic distance, such as F-statistics, and the number of migrants (N_m) between sampling groups or populations.

Little information exists on the site faithful and migratory behaviors of all three species of mergansers that breed and winter across North America. Instead, much of what is known comes from research that has investigated the impact of these species on wild fish stocks (Wood and Hand 1985, Svenning et al. 2005) as Red-breasted (*Mergus serrator*) and Common Merganser (*M. merganser*) are both general piscine predators (Wiese et al. 2008). Some limited banding data exist for these two species to infer migratory patterns, while substantial banding of Hooded Mergansers (*Lophodytes cucullatus*) has taken place across North American since the 1960s. These long term data are largely the result of sympatric nesting by Hooded Mergansers in areas where nest boxes have been erected for other cavity nesting waterfowl, such as the Wood Duck (*Aix sponsa*). The three species of merganser in North America differ substantially in terms of nesting ecology (Common and Hooded Mergansers nest in cavities, while Red-breasted Mergansers nest on the ground) and the geographic distribution of areas used for breeding and wintering (Dugger et al. 1994, Mallory and Metz 1999, Titman 1999). There has been no previous population genetic work conducted on any of the North American merganser species, and historical banding data have only been summarized for single sites (Dugger et al. 1999).

In this study, I conducted a comparative analysis of all three merganser species in North America using mark-recapture and population genetic data to infer levels of site fidelity within each species to different areas used during the annual cycle, including breeding, molting, and wintering. These investigations not only provided previously undocumented information on the population and migratory characteristics

of these species, but also allowed a test of the genetic implications of philopatry and site fidelity and insight into how assessments of philopatry and site fidelity must be summarized with care.

The specific objectives of this research were to:

1. Draw awareness for the need to return to the original definition of "philopatry" and for caution in assuming that all site faithful behavior results in population structure,
2. Infer general levels of site fidelity with different data types (mark-recapture and genetic) and examine the inherent assumptions and biases of each method that can only be assessed in a comparative context,
3. Infer general patterns of dispersal and migration of each species.
4. Demonstrate that multiple types of populations can exist within a species due to site fidelity, sex-biased dispersal, and seasonal migratory patterns.

CHAPTER 1. Demography, Genetics, and the Value of Mixed Messages[1]

Abstract

Iverson et al. (2004) used estimates of the homing rate for molting adult Harlequin Ducks (*Histrionicus histrionicus*) in Alaska to draw inferences about population structure. Homing rates, defined as one minus the ratio of birds recaptured elsewhere to those recaptured at the original banding site, were high (0.95–1.00) for males and females. Iverson et al. (2004) concluded that these high rates of homing are indicative of demographic independence among molting groups separated by small distances (tens to hundreds of kilometers) and that conservation efforts should recognize this fine-scale population structure. We re-examined their use of the homing rate, because the assumption of equal detection probability across a wide sampling area could have led to an upward bias in their estimates of site fidelity. As a result, we are hesitant to agree with their conclusion of high adult homing to molting areas and that molt-site fidelity is evidence for demographic independence. Our hesitancy stems from the fact that little is known about juvenile and adult movements within and among years, breeding area origins, and the variation of demographic parameters (e.g., survival and productivity) among molting groups. Furthermore, population genetic data of these molting groups suggest gene flow at both nuclear and mitochondrial loci. Such mixed messages between demographic (i.e., banding) and genetic data are increasingly common in

[1]Published as, Pearce, J.M. and S.L. Talbot. 2006. Demography, Genetics, and the Value of Mixed Messages. *The Condor* 108:474–479.

ornithological studies and offer unique opportunities to reassess predictions and make more robust inferences about population structure across broad temporal and spatial scales. Thus, we stress that it is this broader scale perspective, which combines both demography and genetics, that biologists should seek to quantify and conservation efforts should seek to recognize.

Introduction

Structured genetic and demographic patterns are predicted for species that exhibit high levels of natal philopatry (Avise 2004:499). Such patterns are not predicted when natal philopatry is low, even if adults are site faithful, because juvenile dispersal and subsequent reproduction will lead to gene flow among populations (Cabe 1999, Lovette et al. 2004, Arsenault et al. 2005). Yet several molecular examinations of avian species presumed to exhibit natal philopatry (Ransom et al. 2001, Roeder et al. 2001, Kimura et al. 2002, Pearce et al. 2004), or those documented to exhibit high levels of natal philopatry through banding studies (Avise et al. 1992, Birt-Friesen et al. 1992, Austin et al. 1994), have found sampled populations to be largely homogeneous at neutral genetic loci. These mixed messages arise for two general and nonmutually exclusive reasons: differences in the scale of measurement, and dispersal that results in gene flow. First, demographic (i.e., banding) and genetic data assess patterns across very different geographic and temporal scales, thus mixed messages are not restricted to avian taxa (Tallmon et al. 2002, Hauswaldt and Glenn 2005). Genetic methods infer dispersal via gene flow over much larger geographic scales than is usually possible with banding

data. Furthermore, no genetic estimates of dispersal are truly contemporary, but rather represent an average rate of gene flow across multiple generations up to some point in the recent past (Bossart and Prowell 1998). Thus, historical events, such as those related to post-Pleistocene ice movements (Hewitt 2000), can create a condition whereby insufficient time has elapsed since range expansions for natal philopatry to result in genetic differences among populations (Slatkin 1987, Avise 2004). Second, juvenile dispersal and subsequent reproduction results in gene flow among populations (Cabe 1999, Frederiksen et al. 2002, Arsenault et al. 2005). As a result, numerous authors have argued for a combined, multimarker approach to quantify historical and ongoing factors to best infer population patterns (Avise et al. 1992, Bossart and Prowell 1998, Koenig et al. 2000, Kimura et al. 2002, Kendall and Nichols 2004).

Mixed messages have recently confronted researchers investigating molting and wintering groups of Harlequin Ducks (*Histrionicus histrionicus*) in Alaska and British Columbia. Lanctot et al. (1999) used mitochondrial (mt) DNA control region sequence data and nuclear microsatellite loci to characterize molting groups of Harlequin Ducks in southcentral Alaska. Results suggested that sampling areas were largely homogeneous for both types of genetic markers, although slightly higher levels of differentiation were observed between more distant regions using mtDNA. This result was surprising as Cooke et al. (2000) observed adult Harlequin Ducks to exhibit high levels of site fidelity to molting and wintering areas of coastal British Columbia, which they suggested could lead to genetic differentiation of wintering aggregations if mate choice occurs in these locations. Following many years of intensive study, Iverson et

al. (2004) were able to quantify between-year rates of adult molt-site fidelity of Harlequin Ducks in Prince William Sound, Alaska via the homing rate. They observed high homing rates (0.95–1.0) and concluded that these estimates are indicative of demographic independence among molting groups at a finer scale than indicated by genetic data.

Here, we re-examine the homing rate estimator used by Iverson et al. (2004), their conclusion that high male and female adult homing rates are indicative of demographic independence, and offer a review of the distinction between demographic and genetic population structure. One note on terminology: we feel the word 'philopatry' does not adequately apply to nonbreeding areas and that a species is philopatric only if dispersal is limited with respect to an organism's natal area (Greenwood 1980, Shields 1982). Therefore, because Harlequin Ducks in Prince William Sound do not breed where they molt, we use the term 'adult molt-site fidelity' instead of winter philopatry, since Iverson et al. (2004) were concerned with the return of adults to molting areas.

Demography

Iverson et al. (2004) captured and marked molting Harlequin Ducks throughout Prince William Sound, Alaska from 1995 to 1997 and 2000 to 2001. Adult males and females were marked with standard metal leg bands. Hatch year birds were capable of flight and thus unavailable for capture and marking. Banding data were analyzed using an estimator of homing rate, which Iverson et al. (2004:712) define as, "the ratio of birds

recaptured on their original capture site to those recaptured elsewhere (Robertson and Cooke 1999)." This definition of homing rate differs from that given by Anderson et al. (1992), which includes an estimation of fidelity (F), temporary emigration (γ), and recapture (p) given presence. It also differs from the return rate (R), which includes an estimation of survival (S) as well as F, γ, and p (Williams et al. 2002). These estimators can be biased due to confounding among the various parameters, but the direction of the bias is known because noncapture probabilities are estimated. Thus, for the homing rate of Iverson et al. (2004) to accurately quantify fidelity, all marked birds must be recaptured with the same probability regardless of their subsequent molting location (i.e., p cannot vary between birds that return and those that disperse). In other words, the homing rate estimator,

$$SFp_1/(S[Fp_1+(1-F)p_2]),$$

where S drops out, cannot simplify to F unless $p_1 = p_2$. Iverson et al. (2004) acknowledged this assumption and used multiple 'supplementary sites' to document any dispersal events away from the primary Montague Island sites. However, given the fact that most dispersal events detected by Iverson et al. (2004) were of short distances (3.1–8.9 km), our prediction is that dispersal events to supplementary sites >8.9 km should have a lower p than those within 8.9 km of the primary capture locations. Additionally, the longest dispersal event documented via recapture was 51.9 km. Therefore, all Harlequin Ducks within 51.9 km of their initial capture location must have the same probability of recapture following dispersal as those that do not disperse for the assumption of equal capture probability to be met. Thus, the assumption of

equal p across Prince William Sound may not have been appropriate and a lower p for supplementary sites may have resulted in an overestimate of the homing rate at primary sites.

Knowledge of several aspects of movement ecology would enhance the characterization of molt-site fidelity in Harlequin Ducks, such as the distribution of molting birds along Montague Island. Do unsampled molting flocks that could contain marked birds occur close to the three primary sampling areas? What is the number of birds banded at time t, not observed at time $t + 1$, but subsequently observed at time $t + i$? Such data would provide information on detection probabilities, movements among molting sites, and the timing of molt migrations. Also, what is known about the timing of molt for nonbreeding versus brood-rearing females? Are nonbreeding and successfully breeding females equally available for capture during molt drives? Cooke et al. (2000) observed that both younger and older males move among areas and that winter site fidelity may be contingent upon the availability of unpaired females or territoriality of paired males. Thus, information on the number, sex, and age of unbanded birds captured by Iverson et al. (2004) is of interest. Such information seems necessary to fully evaluate the conclusion of Iverson et al. (2004) that molting flocks exhibit high site fidelity and are demographically independent. Demographic independence implies that each molting group is characterized by unique rates of survival and reproduction. If solely males move among molting groups, there is the possibility that population structure exists among females, but nothing is known about the location of breeding areas of female Harlequin Ducks that molt and winter

throughout Prince William Sound. Furthermore, low levels of differentiation among females for maternally inherited mtDNA (see below) suggest that movement among molting areas is not strictly limited to males. In the absence of such information, it is unclear how adult male and female homing rates are indicative of unique demographic and thus conservation units at such a small scale.

Genetics

Behavioral traits of waterfowl have led to various hypotheses about the location and degree of population genetic structure. First, in most waterfowl species females exhibit greater natal and breeding site fidelity than males (Greenwood 1980, Anderson et al. 1992). Over sufficient periods of time and spatial scale, natal philopatry can lead to genetic differentiation, especially at maternally inherited molecular loci such as mtDNA. Second, both sexes may exhibit winter site fidelity for a variety of ecological and genetic reasons, including re-establishment of breeding pairs as mate choice is thought to occur on the wintering grounds (reviewed by Robertson and Cooke 1999). In either case adult nest or winter site fidelity might also serve to differentiate populations, but only at larger scales where populations are separated at distances greater than all dispersal events. However, even at these larger scales, genetic differentiation can be limited by historical demographic processes and large effective population sizes, which reduces the diversifying forces of mutation and drift (reviewed by Avise 2004).

In Harlequin Ducks, molt-site fidelity would only lead to demographic and

population genetic structure if molting flocks remain as distinct units throughout the entire year. Regehr et al. (2001) observed that Harlequin Duck broods may accompany adult females to molting sites. However, it is not known if juvenile Harlequin Ducks, especially females, return to these same molting areas as adults in subsequent years. Tracking natal dispersal of birds via mark-recapture methods is very difficult because efforts must be made to recapture previously marked individuals across a wide range of possible dispersal distances. This difficulty is compounded among sea duck species, which typically do not breed until their second or third year. Thus, data from multiple years and wide geographical efforts would be needed to discern the range of possible dispersal events (see Lebreton et. al. 2003). However, if dispersal is male-biased, one might predict higher levels of population differentiation using maternally inherited mtDNA in contrast to nuclear DNA, which tracks both maternal and paternal lineages. Lanctot et al. (1999) observed precisely this pattern, with slightly elevated levels of differentiation for mtDNA in comparison to nuclear microsatellite data among regional groupings of female Harlequin Ducks. Still, the level of mtDNA differentiation observed by Lanctot et al. (1999) was low ($\Phi_{ST} = 0.05$) suggesting some female gene flow, but at a reduced level compared to males.

Cooke et al. (2000) viewed the genetic data of Lanctot et al. (1999) as validation of their conclusions of male-mediated gene flow, but Iverson et al. (2004) found the genetic data unable to "indicate" the fine-scale population structure suggested by the homing rate. First, little is known about the breeding area origins of molting Harlequin Ducks in Prince William Sound. Genetic data would only indicate fine-scale structure

if each molting flock remained isolated throughout the year and over thousands of generations. A more likely scenario is that each molting flock is composed of birds from multiple breeding areas. Second, consider the genetic implications of demographic independence on such a fine scale. If juveniles follow females to molting sites each year and then both sexes continually return to those sites each year at a homing rate of 0.95–1.0 (Iverson et al. 2004), two immediate predictions for these flocks are: (1) elevated levels of inbreeding within each "demographically independent" molting flock, and (2) substantially higher levels of mtDNA population differentiation due to the smaller effective population size of mtDNA compared to nuclear loci and the small size of each molting flock ($n \approx 30$), compounding genetic drift. Neither of these predictions is borne out by Lanctot et al. (1999). Genotype data from five microsatellite loci showed no significant heterozygote deficiencies, inbreeding coefficients did not differ significantly from zero, and levels of population differentiation estimated using mtDNA were low.

Other hypotheses concerning the population genetics of wintering Harlequin Ducks in Prince William Sound include: (1) a lack of power among genetic markers to distinguish wintering groups, (2) insufficient time since populations expanded into northern latitudes for site fidelity patterns to accrue genetic differences, and (3) molt-site fidelity is a complex behavioral process. A lack of power seems unlikely because fewer genetic loci have shown population differentiation in other waterfowl that exhibit high levels of adult site fidelity (Pearce et al. 2000). Harlequin Ducks have likely experienced historical population growth and expansion since the last glacial

maximum. Consistently low levels of nucleotide diversity (near zero) across populations, as observed by Lanctot et al. (1999), are indicative of sudden population growth and expected if time is sufficient for recovery of haplotype variation via mutation, but too short for the accumulation of differences among sequences (reviewed by Avise 2000). Lastly, Lanctot et al. (1999) correctly acknowledged that movements of sub-adult birds among molting sites before patterns of adult fidelity are established might nullify the effects of high adult fidelity to these same sites (as observed in other species; Cabe 1999, Arsenault et al. 2005). No increase in DNA samples or genetic loci would recover a signal of population differentiation if natal and adult dispersal occur among these molting groups. Such movements would also erode any demographic independence among these same groups.

The hypothesis of molt or winter site fidelity leading to demographic and genetic structure deserves further examination because anthropogenic effects on sea duck populations often occur on the wintering grounds (Flint et al. 1999, Esler et al. 2000, Camphuysen et al. 2002). However, recent work suggests little genetic evidence for population structure among wintering sea ducks at either regional (Lanctot et al. 1999) or continental scales (Pearce et al. 2004). Additionally, the literature presented by Iverson et al. (2004) does not support a hypothesis that strong affiliations to nonbreeding areas are common among sea duck species. Papers by Alison (1974) and Savard (1985) are each based upon a single marked bird and Limpert (1980) estimated a homing rate of 39%. Of 26 male and two female Harlequin Ducks banded by Breault and Savard (1999), nine males were seen at the same location in the following year,

while two males were seen at an adjacent molting site. Thus, this and other literature (Cooke et al. 2000, Flint et al. 2000, Hatton and Marquiss 2004, Mehl et al. 2004) suggests that annual affiliations to molting areas by sea ducks are quite variable. Lastly, we view molt-site fidelity a less than robust measure of population structure without evidence that molting flocks originate from distinct breeding areas. Under the scenario that molting flocks are composed of birds from a variety of breeding areas, fidelity is instead an intriguing behavioral pattern and not a measure of demographic independence.

The Value of Mixed Messages

Conservation plans often seek to delineate geographic or taxonomic units as distinct population segments to effectively monitor status and trends (U.S. Fish and Wildlife Service and National Marine Fisheries Service 1996). Defining such units relies upon a wide array of criteria that for migratory birds may include morphological or plumage characteristics, demographic patterns quantified by banding or radio-telemetry, molecular genetic data, or geographic separation of population segments during the annual cycle. However, focusing on only one type of data to define such units misdirects valuable research and conservation efforts (Zink et al. 2000) and tends to promote population structure as a binary condition: populations are either structured or they are not (Crandall et al. 2000). A larger set of direct and indirect markers are now available for assessing movement patterns (reviewed by Webster et al. 2002, Kendall and Nichols 2004), as well as novel analytical methods that *estimate* levels,

directionality, and sources of variation in dispersal rather than simply *testing* dispersal as a binary condition (Pritchard et al. 2000, Hey and Nielsen 2004, Kendall and Nichols 2004). Thus, we wish to stress that behavioral patterns among avian populations are intricate and idiosyncratic (Avise et al. 1992, Zink et al. 2003, Coltman 2004) and efforts should focus on the robust quantification of these multifaceted processes with as much information as possible.

For example, a number of avian genetic studies discuss the impact of historical demographic processes on levels of population differentiation and the need for other, nongenetic data to verify or challenge conclusions (Bossart and Prowell 1998, Kimura et al. 2002, Pearce et al. 2005). Similarly, banding studies have called for DNA-based estimates of movement after recognizing the difficulty of detecting and quantifying long-distance dispersal (Koenig et al. 2000, Arsenault et al. 2005). In a joint analysis of banding and genetic data for the Lesser Snow Goose (*Anser caerulescens*), Avise et al. (1992:1094) argued appropriately that "both evolutionary (genetic) and contemporary (behavioral) perspectives are required for a full appreciation of the geographic population structure of a species."

An examination of the table of contents of recent ornithological and molecular ecology journals reveals the current focus on demographic parameters (e.g., nesting success, productivity, survival, dispersal, and colonization history) and their role in population status and trends. Yet a common misconception is that genetic data are a panacea for inferring population structure. Instead, molecular genetic markers should be viewed as offering a singular but multifaceted perspective on population

differentiation and demography. Regardless of whether genetic or nongenetic methods are used, we encourage researchers to use multiple data types when they are available. Even in cases where genetic data suggest no differentiation among sampling locales, such as among molting groups of Harlequin Ducks, there is still a wealth of information that can be inferred from the molecular information, such as historical population trends (Emerson et al. 2001), geographic variation in genetic diversity (Busch et al. 2000, Zink et al. 2000), relative levels of female natal philopatry and male dispersal (Pearce et al. 2005), or evidence for gene flow via dispersal that is difficult to assess with localized banding data (Arsenault et al. 2005). Because inferences from multiple markers reveal the weaknesses and strengths of each method, comparisons among data types provide a competing model framework to reassess predictions, evaluate temporal and spatial scales, and best infer population patterns.

Literature Cited

Alison, R. M. 1974. Oldsquaw homing in winter. Auk 91:188.

Anderson, M. G., J. M. Rhymer, and F. C. Rowher. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. *In* Ecology and management of breeding waterfowl, pp. 365–395. (B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds). University of Minnesota Press, Minneapolis.

Arsenault, D. P., P. B. Stacey, and G. A. Hoelzer. 2005. Mark-recapture and DNA fingerprinting data reveal high breeding-site fidelity, low natal philopatry, and low levels of genetic population differentiation in Flammulated Owls (*Otus flammeolus*). Auk 122:329–337.

Austin, J. J., R. W. White, and J. R. Ovenden. 1994. Population-genetic structure of a philopatric, colonially nesting seabird, the Short-tailed Shearwater (*Puffinus tenuirostris*). Auk 111:70–79.

Avise, J. C. 2000. Phylogeography: the history and formation of species. Harvard University Press, Cambridge, Massachusetts.

Avise, J. C. 2004. Molecular markers, natural history and evolution. Second edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Avise, J. C., R. T. Alisauskas, W. S. Nelson, and C. D. Ankney. 1992. Matriarchal population genetic structure in an avian species with female natal philopatry. Evolution 46:1804–1096.

Birt-Friesen, V. L., W. A. Montevecchi, A. J. Gaston, and W. S. Davidson. 1992. Genetic structure of Thick-billed Murre (*Uria lomvia*) populations examined using direct sequence analysis of amplified DNA. Evolution 46:267–272.

Bossart, J. L., and D. P. Prowell. 1998. Genetic estimates of population structure and gene flow: limitations, lessons and new directions. Trends in Ecology and Evolution 13:202–206.

Breault, A. M., and J-P. L. Savard. 1999. Philopatry of Harlequin Ducks molting in southern British Columbia. *In* Behavior and ecology of sea ducks, pp. 41–44. (R. I. Goudie, M. R. Petersen, and G. J. Robertson, Eds.). Canadian Wildlife Service Occasional Paper, Ottawa, Canada.

Busch, J. D., M. P. Miller, E. H. Paxton, M. K. Sogge, and P. Keim. 2000. Genetic variation in the endangered southwestern Willow Flycatcher. Auk 117:586–595.

Cabe, P. R. 1999. Dispersal and population structure in the European Starling (*Sturnus vulgaris*). Condor 101:451–454.

Camphuysen, C. J., C. M. Berrevoets, H. J. Cremers, A. Dekinga, R. Dekker, B. J. Ens, T. M. van der Have, R. K. Kats, T. Kuiken, and M. F. Leopold. 2002. Mass mortality of Common Eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. Biological Conservation 106:303–317.

Coltman, D. W. 2004. Differentiation by dispersal. Nature 433:23–24.

Cooke, F., G. J. Robertson, C. M. Smith, R. I. Goudie, and W. S. Boyd. 2000. Survival, emigration, and winter population structure of Harlequin Ducks. Condor 102:137–144.

Crandall, K. A., O. R. P. Bininda-Emonds, G. M. Mace, and R. K. Wayne. 2000. Considering evolutionary processes in conservation biology. Trends in Ecology and Evolution 15:290–295.

Emerson, B. C., E. Paradis, and C. Thebaud. 2001. Revealing the demographic histories of species using DNA sequences. Trends in Ecology and Evolution 16:707–716.

Esler, D., J. A. Schmutz, R. L. Jarvis, and D. M. Mulcahy. 2000. Winter survival of adult female Harlequin Ducks in relation to history of contamination by the *Exxon Valdez* oil spill. Journal of Wildlife Management 64:839–847.

Flint, P. L., A. C. Fowler, and R. F. Rockwell. 1999. Modeling bird mortality associated with the *M/V Citrus* oil spill off St. Paul Island, Alaska. Ecological Modelling 117:261–267.

Flint, P. L., M. R. Petersen, C. P. Dau, J. E. Hines, and J. D. Nichols. 2000. Annual survival and site fidelity of Steller's Eiders molting along the Alaska Peninsula. Journal of Wildlife Management 64:261–268.

Fredericksen, M., T. Bregnballe, M. R. van Eerden, S. van Rijn, and J. D. Lebreton. 2002. Site fidelity of wintering cormorants *Phalacrocorax carbo sinensis* in Europe. Wildlife Biology 8:241–250.

Greenwood, J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior 28:1140–1162.

Hatton, P. L., and M. Marquiss. 2004. The origins of molting Goosanders on the Eden Estuary. Ringing and Migration 22:70–74.

Hauswaldt, J. S., and T. C. Glenn. 2005. Population genetics of the diamondback terrapin (*Malaclemys terrapin*). Molecular Ecology 14:723–732.

Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. Nature 405:907–913.

Hey, J., and R. Nielsen. 2004. Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*. Genetics 167:747–760.

Iverson, S. A., D. Esler, and D. J. Rizzolo. 2004. Winter philopatry of Harlequin Ducks in Prince William Sound, Alaska. Condor 106:711–715.

Kendall, W. L., and J. D. Nichols. 2004. On the estimation of dispersal and movement of birds. Condor 106:720–731.

Kimura, M., S. M. Clegg, I. J. Lovette, K. R. Holder, D. J. Girman, B. Mila, P. Wade, and T. B. Smith. 2002. Phylogeographical approaches to assessing demographic connectivity between breeding and overwintering regions in a Nearctic-Neotropical warbler (*Wilsonia pusilla*). Molecular Ecology 11:1605–1616.

Koenig, W. D., P. N. Hooge, M. T. Stanback, and J. Haydock. 2000. Natal dispersal in the cooperatively breeding Acorn Woodpecker. Condor 102:492–502.

Lanctot, R., B. Goatcher, K. T. Scribner, S. L. Talbot, B. Pierson, D. Esler, and D. Zwiefelhofer. 1999. Harlequin Duck recovery from the *Exxon Valdez* oil spill: a population genetics perspective. Auk 116:781–791.

Lebreton, J. D., J. E. Hines, R. Pradel, J. D. Nichols, and J. A. Spendelow. 2003. Estimation by capture-recapture of recruitment and dispersal over several sites. Oikos 101:253–264.

Limpert, R. J. 1980. Homing success of adult Buffleheads to a Maryland wintering site. Journal of Wildlife Management 44:905–908.

Lovette, I. J., S. M. Clegg, and T. B. Smith. 2004. Limited utility of mtDNA markers for determining connectivity among breeding and overwintering locations in three Neotropical migrant birds. Conservation Biology 18:156–166.

Mehl, K. R., R. T. Alisauskas, K. A. Hobson, and D. K. Kellett. 2004. To winter east or west? Heterogeneity in winter philopatry in a central-arctic population of King Eiders. Condor 106:241–251.

Pearce, J. M., B. J. Pierson, S. L. Talbot, D. V. Derksen, D. Kraege, and K. T. Scribner. 2000. A genetic evaluation of morphology used to identify harvested Canada Geese. Journal of Wildlife Management 64:863–874.

Pearce, J. M., S. L. Talbot, B. J. Pierson, K. T. Scribner, D. L. Dickson, and A. Mosbech. 2004. Lack of spatial genetic structure among nesting and wintering King Eiders. Condor 106:229–40.

Pearce, J. M., S. L. Talbot, M. R. Petersen, and J. R. Rearick. 2005. Limited genetic differentiation among breeding, molting, and wintering groups of the threatened Steller's Eider: the role of historic and contemporary factors. Conservation Genetics 6:743–757.

Pritchard, J. K., M. Stephens, and P. J. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945–959.

Ransom, D., Jr., R. L. Honeycutt, and R. D. Slack. 2001. Population genetics of southeastern Wood Ducks. Journal of Wildlife Management 65:745–754.

Regehr, H. M., C. M. Smith, B. Arquilla, and F. Cooke. 2001. Post-fledging broods of migratory Harlequin Ducks accompany females to wintering areas. Condor 103:408–412.

Robertson, G. J., and F. Cooke. 1999. Winter philopatry in waterfowl. Auk 116:20–34.

Roeder, A. D., R. K. Marshall, A. J. Mitchelson, T. Visagathilagar, P. A. Ritchie, D. R. Love, T. J. Pakai, H. C. McPartlan, N. D. Murray, N. A. Robinson, K. R. Kerry, and D. M. Lambert. 2001. Gene flow on the ice: genetic differentiation among Adelie Penguin colonies around Antarctica. Molecular Ecology 10:1645–1656.

Savard, J-P. L. 1985. Evidence of long-term pair bonds in Barrow's Goldeneye *Bucephala islandica*. Auk 102:389–391.

Shields, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. State University of New York Press, Albany, New York.

Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. Science 236:787–792.

Tallmon, D. A., H. M. Draheim, S. L. Mills, and F. W. Allendorf. 2002. Insights into recently fragmented vole populations from combined genetic and demographic data. Molecular Ecology 11:699–709.

U.S. Fish and Wildlife Service and National Marine Fisheries Service. 1996. Policy regarding the recognition of distinct vertebrate population segments under the Endangered Species Act. Federal Register 61:4721–4725.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology and Evolution 17:76–83.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Estimating survival, movement, and other state transitions with mark-recapture methods, p. 417–493. *In*, Analysis and management of animal populations, pp. 417–493 (B. K. Williams, J. D. Nichols, and M. J. Conroy, Eds.). Academic Press, San Diego, California.

Zink, R. M., G. F. Barrowclough, J. L. Atwood, and R. C. Blackwell-Rago. 2000. Genetics, taxonomy, and conservation of the threatened California Gnatcatcher. Conservation Biology 14:1394–1405.

Zink, R. M., S. V. Drovetski, S. Questau, I. V. Fadeev, E. V. Nesterov, M. C. Westberg, and S. Rohwer. 2003. Recent evolutionary history of the Bluethroat (*Luscinia svecica*) across Eurasia. Molecular Ecology 12:3069–3075.

CHAPTER 2. Site Fidelity is an Inconsistent Determinant of Population Structure in the Hooded Merganser (*Lophodytes cucullatus*): Evidence from Genetic, Mark–Recapture, and Comparative Data[2]

Abstract

The level of site fidelity in birds is often characterized as high on the basis of rates of return or homing from mark–recapture data. For species that exhibit site fidelity, subsequent biological assumptions have included population structure, demographic independence, and that the extirpation of a site-faithful group might be irreversible because of low immigration. Yet several genetic studies have observed patterns of population differentiation that are incongruous with strong site fidelity, which suggests recent isolation, gene flow, or both. Using a 13-year live-recapture and dead-recovery data set, as well as nuclear and mitochondrial DNA collected across the range of the Hooded Merganser (*Lophodytes cucullatus*), an obligate cavity-nester endemic to North America, we found evidence that gene flow persists across portions of the species' range even though the probability of female breeding-site fidelity is high (0.92; 95% confidence interval [CI]: 0.64–0.98) and disjunct breeding ranges of this species have been isolated for ≥ 10,000 years. By combining inferences from genetic, band-recovery, mark–recapture, and comparative data from another cavity-nesting species of

[2]Published as, Pearce, J.M., P. Blums, and M.S. Lindberg. 2008. Site fidelity is an Inconsistent Determinant of Population Structure in the Hooded Merganser (*Lophodytes cucullatus*): Evidence from Mark-recapture, Genetic, and Comparative data. *The Auk* 125:711–722.

waterfowl, we conclude that a high level of site fidelity should not be considered a universal proxy for population structure and demographic independence. Our results also suggest that an accurate assessment of site fidelity—and its implications for population dynamics and delineation—requires cross-species comparisons and multiple data types, such as mark–recapture and genetic information, to best infer patterns across a range of geographic and temporal scales.

Introduction

Structured patterns of genetic differentiation are predicted for species that exhibit natal site fidelity (Avise 2004). Indeed, the historical and theoretical discussions of natal site fidelity (i.e., philopatry)—the behavior of limited dispersal from a birth place—focus on how it promotes inbreeding, why inbreeding might be adaptive, and the idea that limited dispersal may lead to differentiation and speciation (Mayr 1963). However, population structure has also been predicted or assumed for groups of adults that exhibit site fidelity to breeding and non-breeding areas, even though natal areas of these individuals are unknown (reviewed in Pearce and Talbot 2006, Pearce 2007). Several population-genetic examinations of avian species presumed to exhibit natal or adult site fidelity (Ransom et al. 2001, Roeder et al. 2001, Kimura et al. 2002, Peters and Omland 2007) or those documented to exhibit high levels of site fidelity through banding studies (Austin et al. 1994, Burg and Croxall 2004, Van Bekkum et al. 2006) found that sampled populations were largely homogeneous at putatively neutral genetic loci. Such

"mixed messages" can arise for several reasons, including undetected juvenile dispersal, insufficient time since divergence for site fidelity to contribute to population structure, and the inadvertent inclusion of immigrants in assessments of site fidelity (Pearce 2007). Because vital rates, such as annual survival and productivity, can influence population trends (Sæther and Bakke 2000, Blums et al. 2002), the quantification of breeding-site fidelity and its influence on population dynamics and delineation is of wide interest. Additionally, female-biased site fidelity—common among waterfowl (Anatidae)—has significant implications for population structure, especially with mitochondrial DNA (mtDNA), which is inherited through female lineages (Avise et al. 1992, Peters and Omland 2007).

Several assessments of site fidelity have been made for waterfowl species using either mark–recapture or genetic methods (Avise et al. 1992, Lindberg et al. 1998, Blums et al. 2002, Doherty et al. 2002). With mark–recapture methods, estimates of return or homing rates have been used to infer general levels of site fidelity, though these methods are *post-hoc* assessments confounded by mortality and emigration (Doherty et al. 2002). More robust measures of return rates can be obtained through estimation of the fidelity parameter (F), which requires multiple live-recaptures of banded individuals on a given study area, as well as the recovery of banded birds outside that study area and throughout the potential range of dispersal and migration (Burnham 1993, Doherty et al. 2002). Similarly, genetic data have been used as indirect measures of site fidelity and dispersal through estimates of genetic distance (F statistics) and the number of migrants (N_m) between sampling groups or populations.

However, these estimators have been criticized for their unrealistic biological assumptions, such as equal population sizes and symmetrical levels of gene flow (Whitlock and McCauley 1999). More recent estimators include maximum-likelihood and Bayesian methods that have less stringent biological assumptions and infer levels of gene flow and ages of diverged populations (Nielsen and Wakeley 2001). Notably, the "isolation with migration" (IM) coalescent method (Hey and Nielsen 2004) allows assessment of historical versus recent isolation and of migration between groups (see Peters et al. 2005, Omland et al. 2006). Genetic data can also be used to infer demographic processes, such as changes in population size over time (Rogers and Harpending 1992, Emerson et al. 2001).

Here, we apply maximum-likelihood and Bayesian methodologies to live-recapture, band-recovery, and genetic data to evaluate breeding-site fidelity and its effect on population structure in the Hooded Merganser (*Lophodytes cucullatus*). The Hooded Merganser is a secondary cavity-nesting species, relying on tree cavities that are either excavated by other species or formed through tree growth or decay (Dugger et al. 1994). Classified taxonomically as a sea duck (Tribe Mergini), the Hooded Merganser has a disjunct distribution in North America (Fig. 1) and is found in fewer marine habitats than most other members of the sea duck tribe. Patterns of movement and gene flow within and between the disjunct western and central–eastern ranges are not well understood (Dugger et al. 1994), and the historical origins of these ranges are unknown. Fossil records suggest that the Hooded Merganser was likely distributed throughout the central and eastern portion of the present-day United States since the

late Pleistocene (Dugger et al. 1994). Natural and anthropogenic habitat alterations are also thought to have contributed to recent increases in population size and spatial distribution across North America (Heusmann et al. 2000, Davis and Capobianco 2006, Pandolfino et al. 2006). Interestingly, these increases have taken place at a time when other species of sea ducks are in decline (table 2 in North American Waterfowl Management Plan, Plan Committee 2004).

Methods

Band-recovery mapping

To better understand the spatial extent of annual migratory movements of Hooded Mergansers, we examined band-recovery data from the U.S. Geological Survey Bird Banding Laboratory with permission from all active permit holders. We selected band-recovery data from banding areas that were geographically similar to our genetic sampling effort (Fig. 1A, B). Our final data set included information from three states (Maine, Minnesota, and Missouri) and one Canadian province (Ontario) where birds were marked between April and June, 1962–2006. Recovery data from western North America and Louisiana, where we also obtained DNA samples, were not included because they are few. We examined the distribution of 544 band recoveries comprising 399 hatch-year birds (males, females, and unknown sex) and 145 adult females obtained during regular hunting seasons between September and February, 1962–2007. Because approximately half the hatch-year birds were of unknown sex, we did not examine sex-specific recovery patterns. Direct (birds recovered during the first hunting

season after they were banded) and indirect recoveries are also combined, but direct recoveries constituted ≥50% of the total data set for all banding sites (range: 50–67%). All recoveries were dead (i.e., obtained through hunters who shot and reported the band number), and no found-dead or live-recapture information was included. Maps of band recoveries were plotted using ARCMAP, version 9.1 (ESRI, Redlands, California).

Breeding-site fidelity

We used 13 years of live mark–recapture and dead-recovery data to estimate the probability of breeding-site fidelity by adult female Hooded Mergansers to compare with levels of gene flow via molecular methods (below). Between 1994 and 2006, we monitored ~190 nest boxes placed throughout a 112-km^2 area in the Mingo National Wildlife Refuge and adjacent Duck Creek Conservation Area (hereafter "Mingo Swamp") located in southeastern Missouri. In each year, we monitored nest boxes for nesting activity from February to June. At the end of the incubation period, we trapped breeding females and marked day-old ducklings with web tags (1994–1995) or plasticine-filled oval aluminum or stainless steel leg bands (1996–2006; Blums et al. 1994, 1999). Incubating females captured in boxes were examined for the presence of any marker. Females marked with web tags or aluminum plasticine-filled bands were double-banded with a standard metal leg band. An average of 476 day-old ducklings were marked per year between 1994 and 2006, with 4,891 ducklings marked during this 13-year period. Because the sex of ducklings at the time of banding was not determined, we restricted our analysis to 254 adult nesting females captured in nest

boxes, 44% of which (n = 113) were birds known to have hatched on the study area. Thus, we are not estimating natal site fidelity (i.e., philopatry), but breeding-site fidelity of adults, approximately half of which have unknown natal origins.

We formatted capture histories using the live–dead coding in MARK (White and Burnham 1999) and used a grouping variable to assign birds to one of two groups: (1) birds captured in boxes with the presence of a web tag or plasticine band (i.e., natal origin known) or (2) birds captured in boxes with no marks (i.e., natal origin unknown). We used this grouping variable to examine whether birds of unknown natal origin were more likely to have a lower probability of site fidelity than birds known to have hatched on the study area. Sixteen dead recoveries were present in the data set (8 in group 1 and 8 in group 2). We used a Burnham modeling strategy (Burnham 1993, Williams et al. 2002) in MARK, which yields estimates of four parameters: S_i (probability of surviving from year i to year $i + 1$), p_i (probability of capture given presence), r_i (probability of a band being recovered and reported in year i), and F_i (probability of fidelity or returning to the live-recapture study area between year i and year $i + 1$).

We compared competing models with Akaike's information criterion (AIC) adjusted for sample size (AIC_c) and used ΔAIC_c weights (w_i) to determine the strength of support for a particular model (Burnham and Anderson 2002). We examined goodness-of-fit to our data associated with the most general model by calculating a variance inflation factor ($\hat{c}$). No consistent method exists for assessing fit of this class of models. Therefore, we used a bootstrap approach, acknowledging that this may provide a conservative estimate of $\hat{c}$ (Pollock 2002). This inflation factor was calculated

by dividing the deviance of the general model by the mean deviance derived through 500 parametric bootstrap samples created via Monte Carlo simulations in MARK and incorporated as an adjustment to the final model set. Final parameter estimates were obtained via the best approximating model (lowest AIC_c).

DNA sample collection and laboratory methods

To infer levels of gene flow, we collected DNA samples from across the species' breeding and wintering range. Samples of breeding birds came from five areas (Maine and Massachusetts, Minnesota, Missouri, Louisiana, and Ontario) in the central–eastern range (Fig. 1B) and included 123 feathers or egg-shell membranes collected from nest boxes, 14 blood samples from captured birds, and 20 tissue samples. These 20 tissue samples came from the Environment Canada (Wildlife Toxicology Division) Specimen Bank and were collected during breeding months. In the western range, breeding samples were unavailable. Therefore, we used tissue samples from males and females collected during fall and winter months in British Columbia (n = 1), Washington (n = 27), Oregon (n = 15), and California (n = 12). These samples included three museum specimens (University of Washington Burke Museum nos. 58203, 58908, and 63732) and 53 tissue samples from hunters that submitted spread wings to the U.S. Fish and Wildlife Service and Canadian Wildlife Service annual Parts Collection Surveys. Extraction of DNA from all these tissue types followed the methods described in Pearce et al. (2004).

For nuclear genotypic data, we screened 66 available waterfowl microsatellite loci for allele variation in a subset of Hooded Merganser samples. From this initial screening, five loci were selected, including Aphμ2 and Aphμ4 (Maak et al. 2003), CRG (A. Baker pers. comm.), Hhiμ5 (Buchholz et al. 1998), and Mmμ04 (Gautschi and Koller 2005). Polymerase chain reaction (PCR) amplification of microsatellite loci was conducted on a Stratagene 96 Robocycler (La Jolla, California). We also examined several nuclear introns for variation and observed a common polymorphism in the ornithine decarboxylase-7 (OD-7) intron that was characterized by a 19 base-pair (bp) insertion–deletion or indel. Because indels can be informative in both phylogenetic and population genetic contexts (Pearce 2006), we developed PCR primers to characterize the presence or absence of the indel in all Hooded Merganser samples. The PCR primers flanking this indel were OD-7 54F 5'-ACTGTTTTGGCAGAACTG F-3' and OD-7 182R 5'-AGTAACAGCCATTTGAGC-3'. The PCR amplification of all nuclear loci during both screening and data collection involved identical reagent cocktails as described in Pearce et al. (2004), except that all were amplified with the same PCR temperature profile (94°C for 2 min followed by 40 cycles of 94°C for 2 min, 50°C for 1 min, and 72°C for 1 min) using an MJ Research PTC-200 thermal cycler. The PCR products were visualized on 6% polyacrylamide gels using an LI-COR 4200 DNA sequencer (LI-COR Biosciences, Lincoln, Nebraska). Genotypes were scored according to allele size on the basis of an initial comparison to an M13 DNA sequence ladder and then to samples established as size standards that were run on each subsequent gel.

We amplified and sequenced a 437-bp fragment of the control region (domain I) of mtDNA for 134 Hooded Merganser samples using MMCR LH and MMCR LR PCR primers developed for the Goosander (*Mergus merganser merganser*; Hefti-Gautschi et al. 2008). Samples were amplified by PCR and visualized on 5.5% polyacrylamide gels using methods identical to those described by Pearce et al. (2004). Because of the common occurrence of nuclear pseudogenes in avian species (Sorenson and Quinn 1998), we verified that amplified sequences were of mtDNA origin by comparing sequences obtained from heart, blood, and muscle samples from the same individual. Sequences were also compared with a homologous mtDNA region for the Hooded Merganser on GenBank (accession no. AY112958; Donne-Goussé et al. 2002) to ensure similarity. Sequences were aligned using ALIGNIR, version 2.0 (LI-COR Biosciences) and collapsed into unique haplotypes with FABOX (Villesen 2007). All haplotypes reported here have been deposited in GenBank (accession no. EF486446–EF486489).

Genetic diversity

For each microsatellite locus, we calculated allele frequencies, allelic richness (see Kalinowski 2004), and observed (H_o) and expected (H_e) heterozygosity using ARLEQUIN, version 3.0 (Excoffier et al. 2005). ARLEQUIN was also used to conduct exact probability tests for deviations from Hardy-Weinberg equilibrium in each sampling area following the method of Guo and Thompson (1992). We used the program GENEPOP (Raymond and Rousset 1995) to test genotypic linkage

disequilibrium for each pair of loci in each sampling area. Deviations from Hardy-Weinberg were also assessed by estimating Wright's inbreeding coefficient (F_{IS}) across all loci for each sampling area using FSTAT, version 2.9.3 (Goudet 1995). Positive values of F_{IS} indicate heterozygote deficiency, a signal of inbreeding or population admixture (i.e., Wahlund effect), whereas negative values indicate heterozygote excess. For mtDNA sequence data, we used ARLEQUIN to estimate mtDNA haplotype diversity (h; Nei 1987) and the number of variable or segregating sites (s) within each sampling area as indices of genetic diversity. We graphically displayed the relationship of all mtDNA haplotypes using a network diagram constructed in NETWORK, version 4.2 (Bandelt et al. 1999).

Population differentiation and dynamics

To examine continental patterns of genetic differentiation within and between western and central–eastern sampling areas, we used an analysis of molecular variance (AMOVA) in ARLEQUIN to generate estimates of interpopulation variance in nuclear allele (F_{ST}) and mtDNA haplotype (Φ_{ST}) frequency. For mtDNA sequence data, F-statistic analogues were generated using the Tamura and Nei (1993) model of nucleotide evolution as identified by MODELTEST (Posada and Crandall 1998).

We used the isolation with the migration program IM (Nielsen and Wakeley 2001, Hey and Nielsen 2004) to examine whether the disjunct distribution of Hooded Mergansers (Fig. 1) is the result of recent divergence and isolation, gene flow, or both. The IM program uses a Markov-chain Monte Carlo (MCMC) approach to estimate six

demographic parameters: effective population size within each of the two disjunct ranges (θ_{west} and θ_{east}), the ancestral population size at the time of population divergence (θ_A), migration (dispersal that results in gene flow) rates (m) between groups, the time since divergence (t) of the two groups, and the time to most recent common ancestor (TMRCA). We combined samples from all central and eastern locations into a single group to compare with the western group. For initial runs, we assigned wide, flat priors that were assumed to be uninformative for each parameter. We then restricted the range of parameter values around the peaks for final runs. Because estimates of θ_{east}, θ_A, and t did not converge well (i.e., tails of posterior distributions did not approach zero), we ran the program multiple times with different maximum priors for these parameters but found no differences in results. The posterior distribution of TMRCA was used to set final priors for the t parameter. We implemented Metropolis coupling using 10 chains with 10 chain-swap attempts per step, a geometric heating scheme (g1 0.9, g2 0.8), and a burn-in period of 10^6 steps, recording results every hour (see Hey and Nielsen 2004). We ran IM three times under identical conditions, but with different random seeds to assess congruence among runs. Because all three runs gave similar results, we report the peak and 95% CIs of the highest posterior distribution (HPD) of all parameters based on the longest run (31×10^6 steps, >1,000 h, lowest effective sample size = 288). We estimated the effective number of female migrants per generation (M) between western and central–eastern groups using $M = \theta m/2$ (Hey and Nielsen 2004), where θ is the effective population size

of the total population ($\theta_{west} + \theta_{east}$) and m is the migration rate scaled to the neutral mutation rate per generation.

To relate IM estimates to demographic scales, we used a mutation rate (u) of 5.6 $\times 10^{-8}$ substitutions site^{-1} year^{-1} (range 4.8 $\times 10^{-8}$ to 6.9 $\times 10^{-8}$). This estimate is derived from Peters et al. (2005), who estimated a control-region mutation rate of 4.8 $\times 10^{-8}$ for domains I and II in the Wood Duck (*Aix sponsa*). Because our sequence was restricted to domain I, we adjusted our mutation rate using a factor based on the nucleotide diversity of the full fragment of Wood Duck control region (0.0044) compared with the nucleotide diversity of a truncated fragment (0.0052) of identical length to that we obtained for Hooded Mergansers. We then adjusted the mutation rate of Peters et al. (2005) by this factor (1.18) to account for the faster rate of the shorter Hooded Merganser fragment.

Lastly, we calculated mismatch distributions in ARLEQUIN for each sampling area to infer historical population trends and to make direct comparisons with the mismatch distributions of Peters et al. (2005) for the Wood Duck. The mismatch distribution is the observed number of differences between all pairs of haplotypes in the sample (Rogers and Harpending 1992). When the distribution is multimodal, the population is inferred to have maintained a long-term constant size, whereas a unimodal distribution indicates past demographic expansion, with the age of the expansion indicated by the x-axis. The mode of the distribution is expressed by the parameter tau (τ) and can be used to estimate the time to the expansion (t) using the equation $t = \tau / 2\mu$, where μ is the product of the number of nucleotides sequenced (437) and the neutral

mutation rate for domain I of the control region (5.6×10^{-8} substitutions site^{-1} year^{-1}; see above). The 90% CIs of τ were calculated using a parametric bootstrap approach implemented in ARLEQUIN.

Results

Band-recovery mapping

For all banding areas, we observed a general north–south distribution of band recoveries (Fig. 1C–F), though some longitudinal variation is present, especially for the Missouri banding area (Fig. 1E). In northern banding areas (Minnesota, Ontario, and Maine), recoveries occur at progressively more southern latitudes from fall to winter (Fig. 1C, D, F). By contrast, recoveries of both adult and hatch-year birds from the more southern Missouri banding area (Fig. 1E) occur as far north as 49°N latitude (southern Manitoba) and along latitudes near the original banding area during the fall (September–November). Northern recoveries of birds banded in Missouri were not observed during winter months (December–February), perhaps because waterfowl hunting seasons in these areas typically end by 1 January. Direct band recoveries of juveniles were also observed to the west of Missouri in Wyoming and Washington (Fig. 1E).

Fidelity estimation

We captured 254 females or an average of 38 females per year between 1994 and 2006 (range: 20–54 per year). Approximately half (53.7%) of the capture histories were from a single capture event, with 29 females (11.3%) captured >3 times. Eight females were captured in ≥6 of the 13 years. Sixteen dead recoveries of adult females were recorded in October and November, 1995–2006, in either the Mississippi migratory flyway (states of Minnesota, Arkansas, Missouri, and Louisiana) or the Central flyway (South Dakota, Oklahoma, and Texas).

Our final candidate set of models used to estimate the probabilities of survival, recapture, reporting, and fidelity parameters included a total of 11 models. We noted little evidence of overdispersion ($\hat{c} = 1.11$) for the most paramaterized model, $S_{(t)}\, p_{(t)}\, r_{(t)}\, F_{(.)}$, which allowed all parameters except fidelity to vary by time (Table 1); therefore, we did not adjust for lack-of-fit. The best approximating model, $S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{(.)}$, held all parameters constant (no time or group variation). Probability estimates and 95% CIs from this model were as follows: adult female survival (0.72, 0.61–0.82), capture (0.62, 0.55–0.68), reporting (0.08, 0.04–0.12), and fidelity (0.92, 0.64–0.98). We noted some model-selection uncertainty among models 2–4, though all these models received approximately half the support of model 1 on the basis of AIC_c weights (Table 1). Model 2 held all parameters constant except survival, which varied by group. With this model, the difference in survival between group 1 (natal area known) and group 2 (natal area unknown) was small (0.70 ± 0.05 and 0.75 ±0.05, respectively). Model 3 held all

parameters constant except for fidelity, which varied by group. Under this model, fidelity was slightly lower for group 1 (0.89 ± 0.07) than for group 2 (0.94 ± 0.07).

Genetic diversity

A total of 213 Hooded Merganser samples were genotyped for six nuclear loci. Average allelic variation ranged between 2.7 (OD-7) and 11.3 (Aphμ4) alleles, but standardized allelic richness was similar across areas (Table 2). Significant deviations from Hardy-Weinberg (HW) proportions ($P < 0.05$) were detected in 7 of the 30 area-by-locus combinations. No consistent pattern of deviation was noted across all sampling areas, except for the Mmμ04 locus, which exhibited significant heterozygote deficiencies ($P < 0.02$) in three areas (western North America, Maine and Massachusetts, and Minnesota). Exact tests of genotypic equilibrium showed significant values ($P < 0.05$) in 15 of 90 comparisons, but pairs of loci tested were not consistent across sampling areas (data not shown). Six of the 15 significant linkage-disequilibrium tests were observed within the western sampling area, and this was the only area to exhibit a significantly large F_{IS} value (0.147, $P = 0.002$; Table 2), indicating heterozygote deficiency. This result, along with the number of positive tests for linkage disequilibrium in the western group, suggests some heterogeneity among winter samples (i.e., population structure).

A total of 134 Hooded Mergansers from the six sampling areas were sequenced for 437 bp of mtDNA control region (Table 2). Sequences were identical across different tissue types within the same individual Hooded Merganser, which is similar to

a previous mtDNA control-region sequence for this species derived by Donne-Goussé et al. (2002), and were derived primarily from muscle tissue and nest feathers rather than blood. Thus, it is unlikely that DNA fragments amplified in the present study represent nuclear pseudogenes. Forty-four unique mtDNA haplotypes defined by 41 variable sites (all transitions) were identified among the 134 Hooded Mergansers. No gaps or indels were observed. A haplotype network involved numerous hubs and single branches, with no clear phylogeographic clustering of haplotypes either between the disjunct western and central–eastern breeding ranges or among breeding samples within the central–eastern region (Fig. 2). Most mtDNA haplotypes (33 of 44, or 75%) were unique to particular sampling areas, and few were shared among areas.

Population differentiation and dynamics

Overall estimates of F statistics (genetic distance among all areas) were low and nonsignificant for nuclear loci ($F_{ST} = 0.001$, $P = 0.371$) but higher and statistically significant for mtDNA ($\Phi_{ST} = 0.055$, $P < 0.001$). All but one pairwise value of F_{ST} for nuclear data were < 0.010 (Table 3), which suggests greater levels of male-mediated gene flow, as is typical among waterfowl species (Anderson et al. 1992). For mtDNA, significant differences were noted among 6 of 15 comparisons (Table 3), though these did not appear to fit a model of isolation-by-distance. For example, nine haplotypes are shared between the western and central–eastern ranges, but no haplotypes are shared between Missouri and Louisiana (Fig. 2). When we restricted the AMOVA analysis of mtDNA to breeding data (western samples excluded), Φ_{ST} remained essentially

unchanged (0.059, $P < 0.001$), which suggests that greater levels of population structure occur among central–eastern areas as compared with differences between the disjunct ranges.

Parameter estimates from the IM program formed unimodal posterior distributions (Fig. 3), though the tails of distributions for θ_{east} (effective size of central–eastern North America), θ_A (effective size of the ancestral population), and t (time since divergence of the two populations) did not approach zero (Fig. 3B, C). The posterior distribution for t exhibited a smaller peak to the left of the main peak (Fig. 3E). Setting wider priors did not change the locations of peaks in the posterior distributions (not shown). We observed the estimate of θ_{east} to peak at 198.6 (lower 95% HPD: 103.8), and this was 20× the size of the estimate for θ_{west}, which peaked at 10.6 (95% HPD: 6.5–29.0). The posterior distribution of θ_A peaked at 7.9 (95% HPD: 1.6–88.9). The peak estimate for the dispersal rate (m) between western and central–eastern groups was large ($m = 4.0$), and the 95% HPD did not overlap zero (1.0–9.9), which suggests that we could reject the hypothesis of no gene flow (Fig. 3D). Converting these values of m, we estimated the effective number of female migrants per generation (summed over both western and central–eastern groups) to be ~400 (95% HPD: 104.6–1,035.0) between the disjunct ranges. The parameter distribution for t peaked at 1.4 (95% HPD: 0.3–7.5). Converting this estimate of t to time in years suggests that the disjunct ranges of the Hooded Merganser split ~57,000 years ago (range: 10,000–357,000 years). The parameter distribution for TMRCA peaked at 2.3 (95% HPD: 1.4–3.7).

The observed mismatch distributions were unimodal (Fig. 4) and had similar modes for both western ($\tau = 3.09$; 95% CI: 1.5–5.6) and central–eastern samples ($\tau = 3.48$; 95% CI: 1.7–6.6), which suggests connectivity (via gene flow) since divergence (see below). On the basis of estimates of τ, we estimated that the entire North American population of Hooded Mergansers began expanding ~60,000 years ago (range: 25,000–157,000).

Discussion

Mark–recapture assessment of site fidelity

Using a joint analysis of live-recapture and dead-recovery, we obtained a high estimate of breeding-site fidelity (~ 0.92) that did not differ between adult females known to have hatched on the study area versus those of unknown natal origins. Similarly high estimates (> 0.75) of the fidelity parameter from Burnham-type models have been observed in other waterfowl species, including the Common Goldeneye (*Bucephala clangula*, another cavity-nesting species; Barker and White 2001) and also for ground-nesting species of waterfowl, including three species of ducks in Europe (Common Pochard [*Aythya ferina*], Tufted Duck [*A. fuligula*], and Northern Shoveler [*Anas clypeata*]; Blums et al. 2002), Northern Pintails (*A. acuta*; Nicolai et al. 2005), and Mallards (*A. platyrhynchos*; Doherty et al. 2002). There is some uncertainty in our estimate of breeding-site fidelity (95% CI: 0.64–0.98) and, thus, the level of fidelity could be lower (i.e., higher emigration).

Adult emigration by females may contribute to underestimates of survival for Hooded Mergansers when estimated by live-recapture information only. Our estimate of female annual survival probability ($S = 0.72$) is higher than that reported by Dugger et al. (1999), who used live-recapture information to estimate a survival probability (Φ) of 0.66 for female Hooded Mergansers. Because Φ is the product of survival and fidelity ($\Phi = SF$), our estimates of survival and fidelity (0.72 and 0.92, respectively) yield an estimate of 0.66 for Φ, which is identical to that obtained by Dugger et al. (1999). It is important to acknowledge that our estimates of survival and fidelity are derived from a sample of nest boxes and, thus, may not be representative of birds nesting in natural cavities. Hooded Mergansers rely on tree cavities that are either excavated by other species or formed through tree growth or decay, but cavity availability across the landscape is unknown (but see Aitken et al. 2002).

Genetic assessment of site fidelity

An expected outcome of high site fidelity by female waterfowl is population genetic differentiation, especially for mtDNA. However, we found four lines of genetic evidence that suggest female-mediated dispersal, by both juveniles and adults, may be more frequent than expected in the Hooded Merganser. First, we observed that some pairwise comparisons of sampling areas exhibit elevated levels of mtDNA differentiation, especially among breeding areas in the central–eastern range of the species (Table 3). However, these and continent-wide patterns of mtDNA distance do

not fit a model of isolation-by-distance, especially between the disjunct western and central–eastern ranges.

Second, we observed a lack of clustering of similar haplotypes by breeding area (Fig. 2), as is expected if dispersal is limited among areas. Third, nearly identical mismatch distributions of western and central–eastern ranges (Fig. 4) suggest a common population history and that the two ranges may not be demographically independent. An alternative explanation to the above three patterns is that Hooded Mergansers have experienced one or several periods of population splitting (vicariance) and expansion followed by zero gene flow, which has resulted in stochastic mtDNA lineage sorting and similar mismatch distributions across the continent. However, our IM analysis is in conflict with this alternative explanation, in that it suggests that gene flow is necessary to explain patterns of genetic variation between western and central–eastern ranges. Additionally, the IM analysis suggests that the disjunct ranges of the Hooded Merganser split ~57,000 years ago (but perhaps as recently as 10,000 years ago), and this time-span is sufficient to structure mtDNA patterns in another cavity-nesting species of waterfowl that is also endemic to North America.

Comparative assessment

Peters et al. (2005) examined mtDNA variation across the range of the Wood Duck, which also has a disjunct breeding and wintering range similar to that of the Hooded Merganser, is an obligate cavity-nester, and exhibits female breeding-site fidelity (Ransom et al. 2001). Peters et al. (2005) observed that the level of mtDNA genetic

differentiation in Wood Ducks was nearly an order of magnitude greater (Φ_{ST} = 0.31) between disjunct western and eastern ranges than we report in Hooded Mergansers (Φ_{ST} = 0.05). In an IM analysis of their data, Peters et al. (2005) observed similar peak values to those of Hooded Mergansers for nearly all parameters, except 0_{west} and *m*, which were lower in Wood Ducks (Fig. 3). Peters et al. (2005) also found that the 95% CI for the migration parameter (*m*) in Wood Ducks overlaps zero and suggested that the data were consistent with divergence followed by complete isolation of western and eastern groups. By contrast, our IM analysis rejected complete isolation following divergence (i.e., the 95% limits on the posterior distribution for *m* did not overlap zero). In other words, the probability of no gene flow is very low, even though the disjunct ranges of the Hooded Merganser split within approximately the same time-frame as the Wood Duck (Fig. 3). Furthermore, the mtDNA haplotype networks for these two species are dissimilar, and no haplotypes are shared between western and eastern ranges of the Wood Duck as is observed in the Hooded Merganser.

Mismatch distributions also differ between the Wood Duck and Hooded Merganser and likely arise because of the different dispersal tendencies for these two species. In the Wood Duck, both population stability and growth were observed in western and eastern North America, respectively, which suggests limited dispersal and independent demographic histories since population divergence (fig. 4 in Peters et al. 2005). Furthermore, the timing of population expansion for eastern Wood Ducks (τ = 3.4) and for the two ranges of Hooded Mergansers (τ = 3.1 and 3.5; Fig. 4) are similar. Taken together, we conclude that the disjunct ranges of the Wood Duck and Hooded

Merganser split within similar time-frames, but a higher rate of dispersal and emigration in the Hooded Merganser results in dissimilar genetic patterns when comparing the two species. Average dispersal distances of juvenile Hooded Mergansers are unknown, but direct recoveries of juveniles (Fig. 1) suggest that they can cross large distances after fledging. Greater movement probability among Hooded Mergansers is also evident from the geographic distribution of >600 recoveries of both Wood Duck and Hooded Merganser ducklings banded at hatch in Missouri. Of these recoveries, the proportion of northward, long-distance (>500 km) movements by Hooded Mergansers was nearly 5× that for Wood Ducks (27% and 5%, respectively). Additionally, most of the Hooded Merganser recoveries in this data set came from areas far north of Missouri (e.g., Great Lakes area) during the first autumn following hatch (Fig. 1E), but no direct recoveries of young Wood Ducks were obtained from these northern areas (P. Blums unpubl. data).

We lack the data to assess whether dispersal in the Hooded Merganser varies annually or geographically, but this also may explain the variation in levels of mtDNA differentiation across North America. Both Blums et al. (2002) and Nicolai et al. (2005) found a positive trend between habitat quality and fidelity rate in four other waterfowl species, and geographic variation in fidelity was observed among hatch-year Mallards by Doherty et al. (2002). Annual or geographic variation in dispersal, emigration, and cavity availability may also contribute to recent observations of population and range expansions of Hooded Mergansers across North America (Heusmann et al. 2000, Davis and Capobianco 2006, Pandolfino et al. 2006). Thus, both fidelity and dispersal have

likely contributed to the stochastic pattern of mtDNA differentiation across the North American range of the Hooded Merganser. That is, through periods of random dispersal and colonization, the same mtDNA lineages could sort (via both extinction and fixation) to high frequencies in some subpopulations, but not in others. This stochastic effect could result in some subpopulations being genetically similar, whereas others are quite different regardless of the geographic distance between them. However, by combining inferences from mark–recapture, band-recovery, and genetic and comparative assessments, we are able to more conclusively show that female natal and breeding-site fidelity are lesser factors than juvenile dispersal and adult emigration by females for explaining the current mtDNA haplotype distribution of the Hooded Merganser.

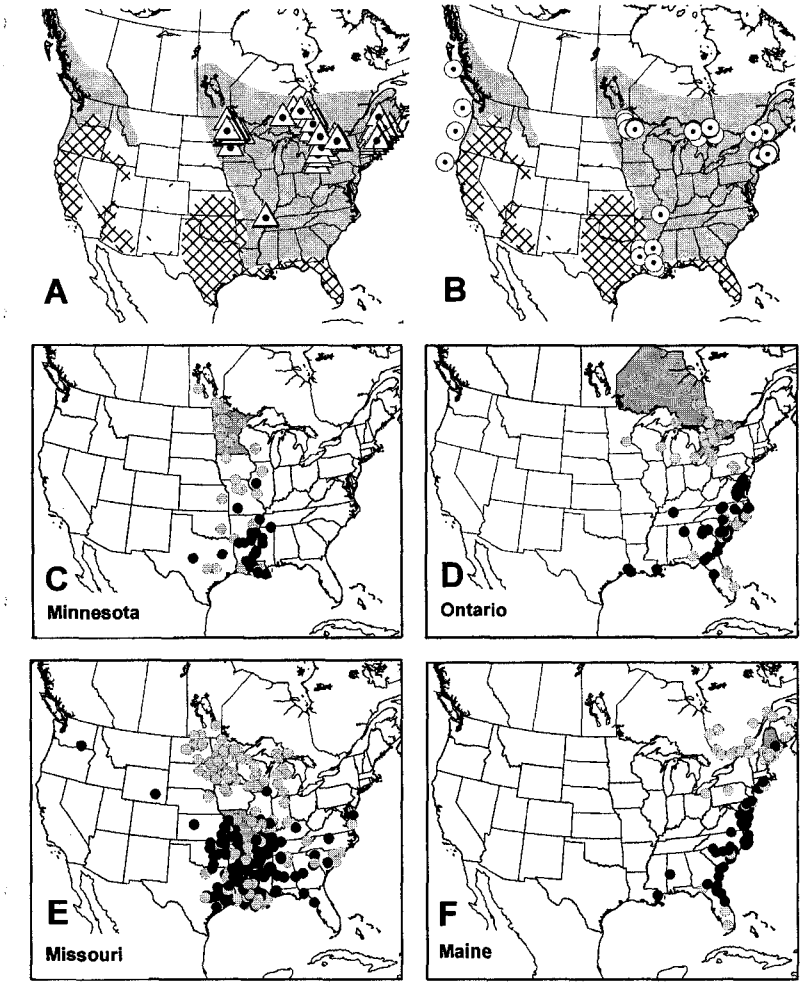

Figure 1. Locations of banding locations (A), DNA sampling locales (B) and band recoveries (C–F). Maps A and B show the North American wintering (cross-hatch) and year-round (gray) distribution of the Hooded Merganser. Triangles in map A depict banding locations used for mapping band recoveries in Minnesota, Ontario, Missouri, and Maine (maps C–F). Circles in map B show distribution of DNA collection locales, and each circle represents >1 sample (see Table 2). In maps C–F, the banding state or province is shaded and recovery locations are coded by season: September–November (gray dots) and December–January (black dots).

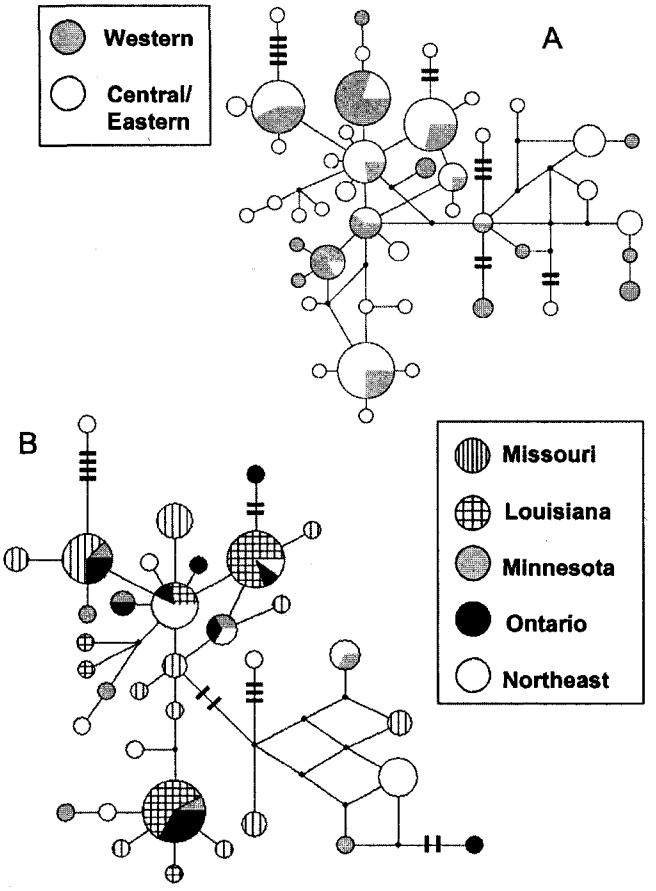

Figure 2. MtDNA haplotype networks for (A) individuals sampled within western and central-eastern areas and (B) within the central-eastern area only. A single site substitution links each circle except where bars are present, which denote multiple substitutions between haplotypes. Circles are drawn proportionally to observed number of each haplotype. Small black dots are inferred haplotypes.

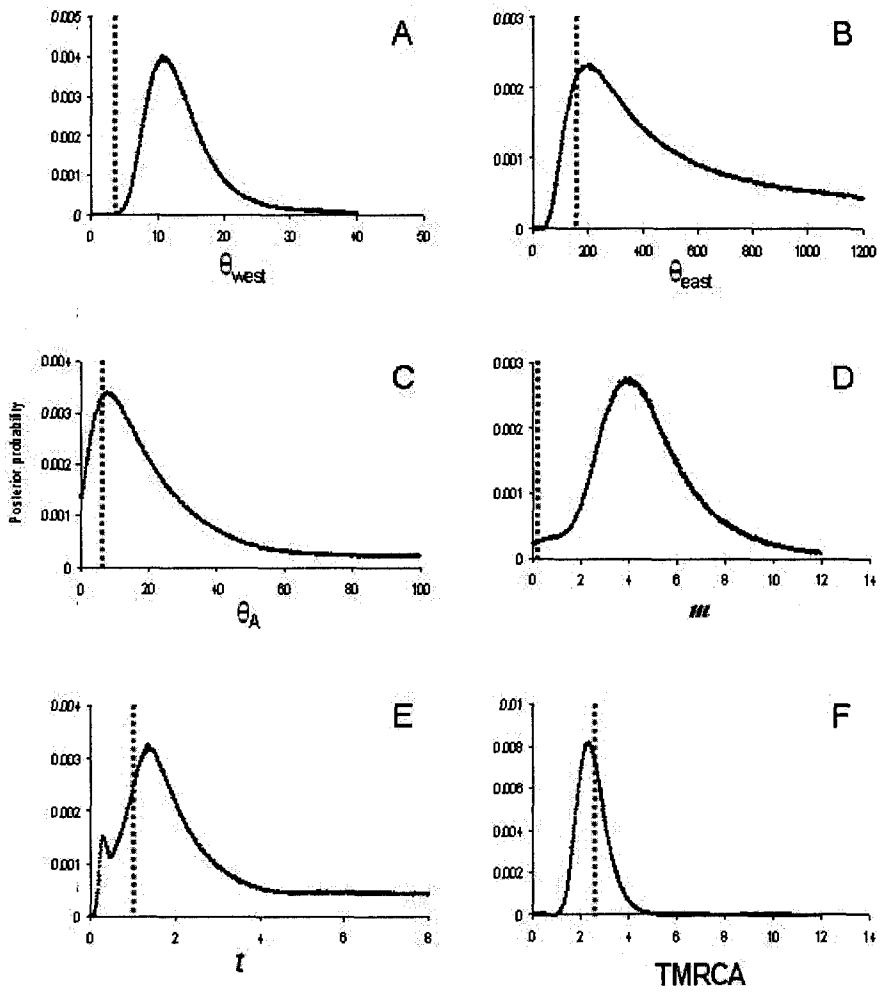

Figure 3. Posterior likelihood distributions from the IM program showing parameter estimates for all sampled haplotypes. Parameters include (A) θ_{west} (effective size of western North America), (B) θ_{east} (effective size of central–eastern North America), (C) θ_A (effective size of the ancestral population), (D) *m* (migration rate), (E) *t* (time since divergence of the western and central–eastern samples, and (F) time to most recent common ancestor (TMRCA). For comparison, the dashed vertical lines show the peak estimates for Wood Ducks for each IM parameter as estimated by Peters et al. (2005).

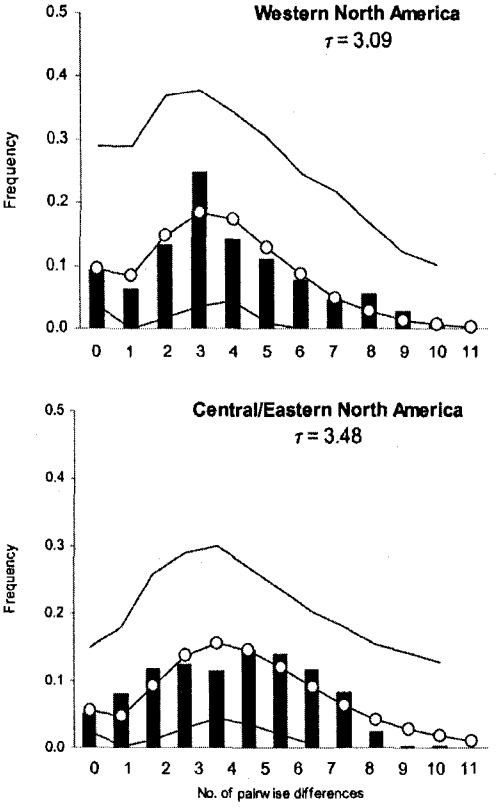

Figure 4. Mismatch distributions of mtDNA sequence data and estimates of expansion (τ) parameter for western and central–eastern samples of Hooded Mergansers. Black bars represent observed pairwise distributions between haplotypes, and solid lines with circles represent a model of spatial range expansion. Solid lines show 95% confidence intervals for the range-expansion model.

Table 1. Mark-recapture models used to estimate probabilities of site fidelity (F), survival (S), capture (p), and reporting (r) of adult female Hooded Mergansers banded at Mingo Swamp, Missouri (1994–2006).

Model[a]	Deviance[b]	Parameters	ΔAIC_c	w_i[c]
1. $S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{(.)}$	444.84	4	0.00	0.31
2. $S_{(g)}\, p_{(.)}\, r_{(.)}\, F_{(.)}$	443.78	5	0.98	0.19
3. $S_{(.)}\, p_{(.)}\, r_{(.)}\, F_{(g)}$	444.26	5	1.45	0.15
4. $S_{(.)}\, p_{(.)}\, r_{(g)}\, F_{(.)}$	444.72	5	1.91	0.11
5. $S_{(g)}\, p_{(.)}\, r_{(.)}\, F_{(g)}$	443.64	6	2.89	0.07
6. $S_{(g)}\, p_{(.)}\, r_{(g)}\, F_{(.)}$	443.71	6	2.95	0.07
7. $S_{(.)}\, p_{(g)}\, r_{(g)}\, F_{(.)}$	444.63	6	3.87	0.04
8. $S_{(g)}\, p_{(g)}\, r_{(g)}\, F_{(.)}$	443.71	7	5.01	0.02
9. $S_{(g)}\, p_{(g)}\, r_{(g)}\, F_{(g)}$	443.61	8	6.98	0.00
10. $S_{(t)}\, p_{(.)}\, r_{(.)}\, F_{(.)}$	435.63	16	15.83	0.00
11. $S_{(t)}\, p_{(t)}\, r_{(t)}\, F_{(.)}$	416.38	39	48.25	0.00

[a]Model parameters were constant (.) and varied by year (t) or by group (g), where group 1 were adults known to have hatched on the study area and group 2 were of unknown natal origins. AIC_c for model 1 was 1,090.01.

[b]The difference between –2log(likelihood) of the current model and –2log(likelihood) of the saturated model.

[c]Model weights or probability that model i is the best fit for the data.

Table 2. Summary statistics for mtDNA sequence and six nuclear loci by sampling area, including number of individuals, N (and number of mtDNA haplotypes per site), allelic richness (A) averaged across loci, haplotype diversity (h), number of segregating sites (s), and average expected (H_E) and observed (H_O) heterozygosities across all nuclear loci.

	Sampling area					
	Western North America[a]	Minnesota	Missouri	Louisiana	Ontario	Massachusetts and Maine
MtDNA						
N	49 (17)	9 (9)	23 (12)	20 (7)	14 (10)	19 (11)
h (s)	0.90 (20)	1.0 (18)	0.92 (20)	0.76 (11)	0.92 (15)	0.90 (22)
Nuclear loci						
N (A)	56 (4.8)	27 (5.0)	35 (4.5)	37 (4.7)	20 (4.3)	38 (4.7)
H_E / H_O	0.65/0.55	0.64/0.57	0.64/0.59	0.66/0.61	0.62/0.57	0.65/0.59
F_{IS} [b]	0.15**	0.12	0.08	0.08	0.07	0.09

*$P < 0.05$, **$P < 0.01$.

[a]Includes samples from British Columbia, Washington, Oregon, and California.

[b]Positive values of F_{IS} indicate heterozygote deficiency.

Table 3. Pairwise *F*-statistics across sampling areas for Hooded Mergansers based on mtDNA sequence data (above diagonal) and nuclear genotypic data (below diagonal)[a]. Overall estimates of *F*-statistics for nuclear and mtDNA data were 0.001 and 0.055, respectively.

	Western North America[b]	Minnesota	Missouri	Louisiana	Ontario	Massachusetts and Maine
Western North America		0.022	0.001	0.114**	0.043	0.071**
Minnesota	0.004		0.023	0.044	0.035	0.004
Missouri	0.002	0.002		0.102**	0.016	0.048*
Louisiana	0.001	0.005	0.003		0.016	0.174**
Ontario	0.001	0.010	0.000	0.006		0.090*
Massachusetts and Maine	0.000	0.006	0.012*	0.005	0.006	

*$P < 0.05$, **$P < 0.01$

[a]*F*-statistics of mtDNA data based on a Tamura and Nei (1993) model of nucleotide evolution.

[b]Includes samples from British Columbia, Washington, Oregon, and California.

Literature Cited

Aitken, K. E. H., K. L. Wiebe, and K. Martin. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. Auk 119:391–402.

Anderson, M. G., J. M. Rhymer, and F. C. Rowher. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. Pages 365–395 *in* Ecology and Management of Breeding Waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Austin, J. J., R. W. G. White, and J. R. Ovenden. 1994. Population-genetic structure of a philopatric, colonially nesting seabird, the Short-tailed Shearwater (*Puffinus tenuirostris*). Auk 111:70–79.

Avise, J. C. 2004. Molecular Markers, Natural History, and Evolution. Second edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Avise, J. C., R. T. Alisauskas, W. S. Nelson, and C. D. Ankney. 1992. Matriarchal population genetic structure in an avian species with female natal philopatry. Evolution 46:1084–1096.

Bandelt, H. J., P. Forster, and A. Röhl. 1999. Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16:37–48.

Barker, R. J., and G. C. White. 2001. Joint analysis of live and dead encounters of marked animals. Pages 361–367 *in* Wildlife, Land, and People: Priorities for the 21st Century (R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, Eds.). Proceedings of the Second International Wildlife Management Congress. Wildlife Society, Bethesda, Maryland.

Blums, P., A. Mednis, and J. D. Nichols. 1994. Retention of web tags and plasticine-filled leg bands applied to day-old ducklings. Journal of Wildlife Management 58:76–81.

Blums, P., J. B. Davis, S. E. Stephens, A. Mednis, and D. M. Richardson. 1999. Evaluation of a plasticine-filled leg band for day-old ducklings. Journal of Wildlife Management 63:656–663.

Blums, P., J. D. Nichols, J. E. Hines, and A. Mednis. 2002. Sources of variation in survival and breeding site fidelity in three species of European ducks. Journal of Animal Ecology 71:438–450.

Buchholz, W. G., J. M. Pearce, B. J. Pierson, and K. T. Scribner. 1998. Dinucleotide repeat polymorphisms in waterfowl (family Anatidae): Characterization of a sex-linked (Z-specific) and 14 autosomal loci. Journal of Animal Genetics 29:323–325.

Burg, T. M., and J. P. Croxall. 2004. Global population structure and taxonomy of the Wandering Albatross species complex. Molecular Ecology 13:2345–2355.

Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199–213 *in* Marked Individuals in the Study of Bird Populations (J.-D. Lebreton and P. M. North, Eds.). Birkhauser Verlag, Basel, Switzerland.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach, 2nd ed. Springer-Verlag, New York.

Davis, S., and P. Capobianco. 2006. The Hooded Merganser: A preliminary look at growth in numbers in the United States as demonstrated in the Christmas Bird Count Database. American Birds 60:27–33.

Doherty, P. F., Jr., J. D. Nichols, J. Tautin, J. F. Voelzer, G. W. Smith, D. S. Benning, V. R. Bentley, J. K. Bidwell, K. S. Bollinger, A. R. Brazda, E. K. Buelna, J. R. Goldsberry, R. J. King, F. H. Roetker, J. W. Solberg, P. P. Thorpe, and J. S. Wortham. 2002. Sources of variation in breeding-ground fidelity of Mallards (*Anas platyrhynchos*). Behavioral Ecology 13:543–550.

Donne-Goussé, C., V. Laudet, and C. Hänni. 2002. A molecular phylogeny of Anseriformes based on mitochondrial DNA analysis. Molecular Phylogenetics and Evolution 23:339–356.

Dugger, B. D., K. M. Dugger, and L. H. Fredrickson. 1994. Hooded Merganser (*Lophodytes cucullatus*). *In* The Birds of North America, no. 98 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Dugger, K. M., B. D. Dugger, and L. H. Fredrickson. 1999. Annual survival rates of female Hooded Mergansers and Wood Ducks in southeastern Missouri. Wilson Bulletin 111:1–6.

Emerson, B. C., E. Paradis, and C. Thébaud. 2001. Revealing the demographic histories of species using DNA sequences. Trends in Ecology and Evolution 16:707–716.

Excoffier, L., G. Laval, and S. Schneider. 2005. ARLEQUIN version 3.1: An integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1:47–50.

Gautschi, B., and B. Koller. 2005. Polymorphic microsatellite markers for the Goosander (*Mergus merganser*). Molecular Ecology Resources 5:133–134.

Goudet, J. 1995. FSTAT (version 1.2): A computer program to calculate *F*-statistics. Journal of Heredity 86:485–486.

Guo, S. W., and E. A. Thompson. 1992. Performing the exact test of Hardy-Weinberg proportion for multiple alleles. Biometrics 48:361–372.

Hefti-Gautschi, B., M. Pfunder, L. Jenni, V. Keller, and H. Ellegren. 2008. Identification of conservation units in the European *Mergus merganser* based on nuclear and mitochondrial DNA markers. Conservation Genetics 9: in press.

Heusmann, H. W., T. J. Early, and B. J. Nikula. 2000. Evidence of an increasing Hooded Merganser population in Massachusetts. Wilson Bulletin 112:413–415.

Hey, J., and R. Nielsen. 2004. Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*. Genetics 167:747–760.

Kalinowski, S. T. 2004. Counting alleles with rarefaction: Private alleles and hierarchical sampling designs. Conservation Genetics 5:539–543.

Kimura, M., S. M. Clegg, I. J. Lovette, K. R. Holder, D. J. Girman, B. Milá, P. Wade, and T. B. Smith. 2002. Phylogeographical approaches to assessing demographic connectivity between breeding and overwintering regions in a Nearctic–Neotropical warbler (*Wilsonia pusilla*). Molecular Ecology 11:1605–1616.

Lindberg, M. S., J. S. Sedinger, D. V. Derksen, and R. F. Rockwell. 1998. Natal and breeding philopatry in a Black Brant, *Branta bernicla nigricans*, metapopulation. Ecology 79:1893–1904.

Maak, S., K. Wimmers, S. Weigend, and K. Neumann. 2003. Isolation and characterization of 18 microsatellites in the Peking Duck (*Anas platyrhynchos*) and their application in other waterfowl species. Molecular Ecology Resources 3:224–227.

Mayr, E. 1963. Animal Species and Evolution. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Nei, M. 1987. Molecular Evolutionary Genetics. Columbia University Press, New York.

Nicolai, C. A., P. L. Flint, and M. L. Wege. 2005. Annual survival and site fidelity of Northern Pintails banded on the Yukon-Kuskokwim Delta, Alaska. Journal of Wildlife Management 69:1202–1210.

Nielsen, R., and J. Wakeley. 2001. Distinguishing migration from isolation: A Markov chain Monte Carlo approach. Genetics 158:885–896.

North American Waterfowl Management Plan, Plan Committee. 2004. Implementation Framework: Strengthening the Biological Foundation. Canadian Wildlife Service, U.S. Fish and Wildlife Service, and Secretaria de Medio Ambiente y Recursos Naturales.

Omland, K. E., J. M. Baker, and J. L. Peters. 2006. Genetic signatures of intermediate divergence: Population history of Old and New World Holarctic ravens (*Corvus corax*). Molecular Ecology 15:795–808.

Pandolfino, E. R., J. Kwolek, and K. Kreitinger. 2006. Expansion of the breeding range of the Hooded Merganser within California. Western Birds 37:228–236.

Pearce, J. M. 2006. Minding the gap: Frequency of indels in mtDNA control region sequence data and influence on population genetic analyses. Molecular Ecology 15:333–341.

Pearce, J. M. 2007. Philopatry: A return to origins. Auk 124:1085–1087.

Pearce, J. M., and S. L. Talbot. 2006. Demography, genetics, and the value of mixed messages. Condor 108:474–479.

Pearce, J. M., S. L. Talbot, B. J. Pierson, M. R. Petersen, K. T. Scribner, D. L. Dickson, and A. Mosbech. 2004. Lack of spatial genetic structure among nesting and wintering King Eiders. Condor 106:229–240.

Peters, J. L., W. Gretes, and K. E. Omland. 2005. Late Pleistocene divergence between eastern and western populations of Wood Ducks (*Aix sponsa*) inferred by the 'isolation with migration' coalescent method. Molecular Ecology 14:3407–3418.

Peters, J. L., and K. E. Omland. 2007. Population structure and mitochondrial polyphyly in North American Gadwalls (*Anas strepera*). Auk 124:444–462.

Pollock, K. H. 2002. The use of auxiliary variables in capture–recapture modelling: An overview. Journal of Applied Statistics 29:85–102.

Posada, D., and K. A. Crandall. 1998. MODELTEST: Testing the model of DNA substitution. Bioinformatics 14:817–818.

Ransom, D., Jr., R. L. Honeycutt, and R. D. Slack. 2001. Population genetics of southeastern Wood Ducks. Journal of Wildlife Management 65:745–754.

Raymond, M., and F. Rousset. 1995. GENEPOP (version 1.2): Population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Roeder, A. D., R. K. Marshall, A. J. Mitchelson, T. Visagathilagar, P. A. Ritchie, D. R. Love, T. J. Pakai, H. C. McPartlan, N. D. Murray, N. A. Robinson, K. R. Kerry, and D. M. Lambert. 2001. Gene flow on the ice: Genetic differentiation among Adélie Penguin colonies around Antarctica. Molecular Ecology 10:1645–1656.

Rogers, A. R., and H. Harpending. 1992. Population growth makes waves in the distribution of pairwise genetic differences. Molecular Biology and Evolution 9:552–569.

Sæther, B.-E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Sorenson, M. D., and T. W. Quinn. 1998. Numts: A challenge for avian systematics and population biology. Auk 115:214–221.

Tamura, K., and M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 10:512–526.

Van Bekkum, M., P. M. Sagar, J.-C. Stahl, and G. K. Chambers. 2006. Natal philopatry does not lead to population genetic differentiation in Buller's Albatross (*Thalassarche bulleri bulleri*). Molecular Ecology 15:73–79.

Villesen, P. 2007. FaBox: An online toolbox for FASTA sequences. Molecular Ecology Resources 7:965–968.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement):120–138.

Whitlock, M. C., and D. E. McCauley. 1999. Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm+1)$. Heredity 82:117–125.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press, San Diego, California.

CHAPTER 3. Population Genetic Structure and Migratory Connectivity of Red-Breasted (*Mergus serrator*) and Common Mergansers (*M. merganser*)[3]

Abstract

Genetic markers are useful for inferring patterns of demography of species across broad temporal and spatial scales. When obtained from samples collected across the annual cycle of an organism, genetic data can also be used to assess levels of natal site fidelity (philopatry) and patterns of migratory connectivity between two or more periods of the annual cycle. Using mitochondrial (mt) DNA sequence data from two Holarctic waterfowl species with different nesting ecologies–the Red-breasted Merganser (*Mergus serrator*) and Common Merganser (*M. merganser*)–we tested predictions of population genetic theory resulting from variation in migratory patterns using breeding and wintering samples. Between species, very different mtDNA patterns were evident between breeding samples of the two species, suggesting interspecific differences in dispersal and responses to historical climate change. In contrast, males and females of both species exhibited similarly weak patterns of migratory connectivity with most wintering areas exhibiting mtDNA from multiple breeding areas. Differences in nesting ecology (ground vs. cavity nesting) potentially influenced patterns of female philopatry and, thus, may have played a role in generating different population genetic

[3]Pearce, J.M., K.M. McCracken, T.K. Christensen, and Y.N. Zhuravlev. Population Structure and Migratory Connectivity among Breeding and Wintering Red-breasted (*Mergus serrator*) and Common Mergansers (*M. merganser*). Prepared for submission to *The Auk*.

patterns across breeding areas. Our data offer insights into patterns of male and female migration and dispersal that have implications for assessments of migratory connectivity and the influence of behaviors such as philopatry and site fidelity on population genetic structure.

Introduction

Genetic markers are useful for inferring patterns of demography and migratory behavior of avian species across broad temporal and spatial scales. When used in concert with other data sets, such as mark-recapture, stable isotope, or satellite telemetry, initial predictions from genetic data regarding dispersal and migratory movements can be tested and conflicting conclusions or 'mixed messages' can be assessed (Webster and Marra 2005, Pearce and Talbot 2006). For example, structured patterns of genetic differentiation have been predicted for species that exhibit natal site fidelity or philopatry (Anderson et al. 1992, Pearce 2007). However, juvenile female dispersal prior to the establishment of adult patterns of site fidelity, and historical range expansions, can limit genetic differentiation within and among groups (Milá et al. 2007), even when mark-recapture data suggest a high probability of annual site fidelity (Pearce et al. 2008).

Similarly, quantifying patterns and levels of migratory connectivity (*sensu* Webster et al. 2002, Boulet and Norris 2006) between breeding and nonbreeding areas may be misleading unless dispersal and gene flow are taken into account. For example, Pearce et al. (In Review) observed 'weak' levels of migratory connectivity between

inferred natal areas and subsequent molting locations of Common Mergansers (*Mergus merganser*) in Alaska using mitochondrial (mt) DNA. However, nuclear DNA and band-recovery data suggested that the presence of individuals from multiple breeding areas within molting flocks resulted not only from seasonal migration, but from male dispersal as well. Thus, genetic heterogeneity in nonbreeding groups cannot be used as direct evidence of migratory connectivity between breeding and wintering areas. Instead, an accurate assessment of migratory connectivity, as well as the structure of breeding and wintering groups, may require assessment with multiple, independent data sets.

Using mitochondrial (mt) DNA sequence data from two closely related, Holarctic waterfowl species–the Red-breasted Merganser (*Mergus serrator*) and Common Merganser–we tested predictions of population genetic theory based on migratory patterns. These predictions were based on behaviors common to female waterfowl, such as natal site fidelity (philopatry) and recent band-recovery and satellite telemetry data from both species. Female waterfowl are atypical among birds in that they often return to natal areas for subsequent breeding, and this behavior may lead to population genetic structure, especially for maternally inherited mtDNA (Anderson et al. 1992, Avise et al. 1992). Such behaviors may thus structure breeding female populations of Red-breasted Mergansers and Common Mergansers in similar ways.

Because much of the current breeding distribution of the Red-breasted Merganser occupies habitats exposed during the end of the Pleistocene (Hewitt 2000), we predicted that northward population expansion would lead to an unstructured pattern

of genetic differentiation across their range. In the Common Merganser, we predicted a more elevated level of population structure across North America due to female natal site fidelity as inferred by satellite telemetry data (Pearce and Petersen 2009). For both species, we predicted that levels of migratory connectivity and admixture among breeding groups would vary across North America based on the distribution of wintering areas (Titman 1999, Mallory and Metz 1999) and the geographic variation in migratory tendency, suggested by band-recovery data (Pearce et al. 2005). Additionally, the designation of subspecies of Common Merganser, including one in North America (*M. m. americanus*) and one in Eurasia (*M. m. merganser*), suggests genetic differentiation within and across continents (Mallory and Metz 1999).

Methods

Sampling strategy

To examine population genetic and migratory patterns with mtDNA, we collected breeding and wintering samples across North America and at sites throughout Eurasia, including Greenland, Western Europe, and Russia (Figs. 1 and 2, Appendix). For Red-breasted Mergansers, breeding samples were collected between March and August and came from adult females and pre-fledged young. North American breeding samples included nine feathers or eggshell membranes and 55 tissues. For Common Mergansers, breeding samples were also collected between March and August and came from pre-fledged young, attending adult females, or adult males. These samples included 12 feathers or eggshell membranes and 118 tissues. To examine samples from

southeastern Alaska, we included nine putatively breeding samples of Common Mergansers (two juvenile males, five juvenile females, and two adult females) collected in September and October from Prince of Wales Island, Alaska. Two subadult-plumaged birds (one male from Togiak R., Alaska and one female from Washington), sampled incidentally, were also included to illustrate post-fledging movements (see Results and Discussion). Winter samples (collected between October and January) of both species came from tissues collected by hunters from North America and Eurasia (Figs. 1 and 2, Appendix).

To understand relationships between North American and Eurasian samples of Common Mergansers, we also included mtDNA control region haplotypes for the European Common Merganser (*M. m. merganser*) or Goosander (see Hefti-Gautschi et al. 2008). These sequences included #01 from Switzerland and Italy, #21, #22, #23 from Norway, #30, #31 from Poland, and #33, #35, #36 from Iceland.

DNA extraction, sex determination, and mtDNA sequencing

We extracted DNA from all tissues using an overnight digest at 55°C in a lysis buffer (50mM Tris-HCl pH 8.0, 50 mM EDTA pH 8.0, 1% sodium dodecyl sulfate, 100mM NaCl, and 1% 2-mercaptoethanol). Proteinase K (20mg/ml) was added along with 100mg/ml dithiothrietol (DTT) to feather samples, followed by salt extraction (Medrano et al. 1990). In cases where samples were from birds of unknown sex, we verified it using the P8 and P2 polymerase chain reaction (PCR) primers developed by

Griffiths et al. (1998). We carried out PCR amplifications of the CHD gene in a final volume of 10 μL containing 1.5 μL DNA extract, 10.0 mM Tris-HCl (pH 8.3), 1.5 mM $MgCl_2$, 50.0 mM KCl, 0.01% gelatin, 0.01% NP40, 0.01% Triton-X 100, 0.2 mM deoxyribonucleotide triphosphate (dNTP), 3.6 pmoles unlabeled forward P8 primer, 4.0 pmoles unlabeled reverse P2 primer, 0.4 pmoles labeled P8 primer, 0.1 μg/μL bovine serum albumin, and 0.75 units Taq polymerase (United States Biochemical, Cleveland, Ohio). The PCR cycling was performed on a Stratagene 96 Robocycler (La Jolla, California) using a profile of 94°C for 90 seconds (1 cycle), 40°C for 45 seconds, 72°C for 45 seconds, and 94°C for 30 seconds (40 cycles), 48°C for 60 seconds (1 cycle), and 72°C for 5 minutes (1 cycle). The PCR products were visualized on 6% polyacrylamide gels using a LI-COR 4200 DNA sequencer (LI-COR Biosciences, Lincoln, Nebraska).

We amplified and sequenced 439 and 425 base-pair fragments of the control region (domain I) from Red-breasted Merganser and Common Merganser samples, respectively, using MMCR LH and MMCR LR PCR primers developed for the European Common Merganser (Hefti-Gautschi et al. 2008). Samples were amplified by PCR and visualized on 5.5% polyacrylamide gels using methods described by Pearce et al. (2008). MtDNA sequences were aligned using AlignIR, version 2.0 (LI-COR Biosciences) and collapsed into unique haplotypes using the COLLAPSE function of the FaBox software (Villesen 2007). Because insertion and deletion events ('indels') among mtDNA sequences can be an informative source of nucleotide variation for both phylogenetic and population genetic analyses (Pearce 2006), we

included indels in analyses after first coding them as transitions. All haplotypes derived in this study have been deposited in GenBank under the following accession numbers for Red-breasted Mergansers (FJ191173–FJ191309) and Common Mergansers (FJ190670–FJ190979).

Statistical analyses

We used ARLEQUIN, version 3.11 (Excoffier et al. 2005) to calculate mismatch distributions for breeding samples within North America to infer historical population trends. Mismatch distributions were not generated for Eurasian or wintering samples. The mismatch distribution is the observed number of differences between all pairs of haplotypes in the sample (Rogers and Harpending 1992). When the distribution is multimodal, the population is inferred to have maintained a long-term constant size, whereas a unimodal distribution is indicative of past demographic expansion with the relative age of the expansion (in mutation units) indicated by the *x*-axis.

To assess our initial predictions regarding levels of differentiation for each species, we used both mtDNA haplotype spanning networks, generated by the median-joining method in the program Network, version 4.2 (Bandelt et al. 1999) and ARLEQUIN to examine patterns of genetic differentiation across breeding areas. Levels of Φ_{ST} for mtDNA sequence data were calculated after incorporating the Tamura and Nei (1993) model of nucleotide substitution as identified by MODELTEST (Posada and Crandall 1998) as the best fit to our data.

To assess migratory connectivity between breeding and wintering areas, we used haplotype spanning networks and ARLEQUIN to examine differences between wintering area samples collected in both western and eastern North America. For both species, Φ_{ST} was calculated after first grouping winter samples into three groups: Alaska (Kodiak Island), Western North America (may include Washington, Oregon, California, Arizona, Colorado, Utah, Idaho, and Baja Peninsula), and Eastern North America (may include Nova Scotia, New Foundland, Maine, Massachusetts, New Jersey, Rhode Island, Virginia, Connecticut, and Florida). Inclusion of different localities in each of the three regional groups was dependent upon sampling distribution for each species (see Fig. 1, Appendix).

Additionally, for Common Mergansers we compared winter samples to breeding data collected as part of this study and to a selection of haplotypes from Iceland and Europe obtained by Hefti-Gautschi et al. (2008; see above). We determined mtDNA group membership of Common Merganser winter samples collected across five North American and two Eurasian sites. North American sites included Alaska (Kodiak Island), Western North America (Washington, Oregon, and California), the Intermountain West (Utah, Idaho, Colorado, and Arizona), the Great Lakes area (Minnesota, Wisconsin, and Michigan), and Eastern North America (Pennsylvania, Québec, Newfoundland, and Nova Scotia). Eurasian wintering sites included Denmark and Vladivostok, Russia. MtDNA group membership was conducted by first identifying identical haplotypes using COLLAPSE (Villesen 2007). For new haplotypes not observed among breeding data, we determined mtDNA group

membership using bootstrapped neighbor-joining trees (10,000 replicates) in MEGA, version 4.0 (Tamura et al. 2007) and by constructing haplotype spanning networks of non-matching sequences in relation to breeding sample haplotypes.

Results

Red-breasted Merganser breeding samples

Among 64 North American and Eurasian breeding samples, we observed 25 haplotypes defined by 29 variable sites that were characterized by one transversion and 28 transitions (Table 1). The most common haplotype (#1), was observed in 22% of all samples, including two samples from central Russia, one from Greenland, and two from Scotland. Haplotype #1 was also shared among multiple sampling locations in Alaska (locations #2, 8, and 10; Fig. 3A) and Canada (location #14; Fig. 1). Patterns of mtDNA variation in the Red-breasted Merganser suggest a recent population expansion. The mtDNA haplotype network revealed a star-like toplogy for North American samples with only a single common haplotype (#1, Table 1), from which radiated numerous low frequency haplotypes (Fig. 3A). The mismatch distribution for North American breeding samples was unimodal (Fig. 4A) and not different from a simulated model of expansion (SSD = 0.001, $P = 0.57$). Because of few shared haplotypes among breeding areas (Table 1), an overall significant level of differentiation was observed ($\Phi_{ST} = 0.262$, $P < 0.001$). However, a substantial proportion of the total variation occurred within (73%) rather than between (26%) breeding areas.

Red-breasted Merganser winter samples

Among 75 North American and Eurasian winter samples, 38 haplotypes were observed (not shown). In North America, only six of these haplotypes were identical to those observed in breeding area samples (#1, 2, 7, 8, 9, and 13; Table 1), and they occurred in 29% of winter samples. In the 15 wintering samples from Denmark, only one haplotype matched breeding samples from Scotland (#23; Table 1) and occurred in 40% of samples. Only haplotype #1 was shared among North American and Eurasian wintering samples. Similar to breeding samples, haplotype #1 was most common among winter samples and was observed in Alaska ($n = 3$), Western North America ($n = 3$), Eastern North America ($n = 3$), and Denmark ($n = 1$). In addition to haplotype #1, four haplotypes from Alaska breeding samples (#2, 7, 8, and 9) were observed among wintering birds in Alaska, Oregon, and California, as well as in Maine and Massachusetts. A single breeding area haplotype from Canada (#13) was observed in one wintering bird from New Jersey.

A large proportion of North American (65%) and Danish (53%) wintering samples were novel haplotypes and not assignable to likely breeding areas. In a comparison of haplotype frequencies among three North American wintering areas (Alaska and Western and Eastern North America), we observed an overall significant level of population differentiation ($\Phi_{ST} = 0.101$, $P < 0.001$). However, there was no clear association between haplotype and sampling localities in the haplotype spanning network of North American winter samples (Fig. 5A).

Common Merganser breeding samples

Among 130 North American and Eurasian breeding samples, we observed 32 haplotypes defined by 59 variable sites that were characterized by a single base-pair indel, 4 transversions, and 52 transitions (Table 2). Two transversions each occurred within North America and between North America and European samples. Twenty-nine haplotypes (#1–29) were observed in North American breeding samples and three (#34–37) in breeding samples from Scotland (Table 2). The three haplotypes from Scotland were identical to haplotypes #06 (from Sweden, Finland, and Estonia), #24 (from Norway), and #09 (from Norway, Sweden, and Switzerland) observed by Hefti-Gautschi et al. (2008).

In contrast to Red-breasted Mergansers, Common Merganser breeding samples exhibited a pronounced pattern of population structure. This indirect evidence of female philopatry was found not only in the reciprocal monophyly among distant sampling regions (below), but also at finer geographic scales. For example, we observed independent samples from Fairbanks (n = 10), the Togiak River (n = 5), Anchor River (n = 6) to have identical haplotypes, suggesting shared lineages as a result of long-term philopatry to individual river drainages. North American samples clustered into four groups of haplotypes (Fig. 3B), named hereafter as Beringia (group 1), Alaska, British Columbia (BC), and Prince of Wales Island (group 2), Washington (group 3a) and Western Ontario and Eastern North America (group 3b). Samples from Scotland formed an additional group that differed from North America by an average of

19 site substitutions (Fig. 3B), corresponding to 5.3–7.1% uncorrected sequence divergence (Table 3).

The Beringia group included samples from not only Interior and Western Alaska (locations #20–22, Fig. 2) that are classified as the North American subspecies (*M. m. americanus*), but also the western Aleutian Islands (location #19) and a single sample from near Magadan, Russia (location #18). Common Mergansers in the Aleutian Islands and Russia have historically been classified Goosanders, the Eurasian subspecies (*M. m. merganser*), on the basis of adult male wing plumage (see Gibson and Byrd 2007). Male Goosanders have elongate white secondary wing coverts that cover a black wing bar that is more visible in males from Fairbanks, which do not have the elongate wing coverts. Furthermore, haplotype #3 was found in specimens from both Shemya Island and Fairbanks, Alaska (Table 2, Fig. 2, Appendix), even though males in these areas exhibit two distinct phenotypes. Samples that formed haplogroup 2 came from throughout Southcentral Alaska, Kodiak Island, the Kenai Peninsula, and Prince William Sound, and Prince of Wales Island, Alaska, and Vancouver Island, BC (Fig. 3B).

The haplotype network for breeding samples displayed a close association between samples from Washington (group 3a) and Western Ontario and Eastern North America (group 3b). Multiple inferred haplotypes in the Washington and Eastern North American portion of the network (Fig. 3B) suggest that additional mtDNA variation exists throughout the central portion of North America. The mismatch distribution was multi-modal (Fig. 4B), which is characteristic of samples with deeper coalescence and

multiple periods of divergence (Rogers and Harpending 1992). The overall difference among sampling areas was very high ($\Phi_{ST} = 0.904$, $P < 0.001$), and all pairwise tests were significant, including the smallest difference ($\Phi_{ST} = 0.05$) between Western Ontario and Eastern North America (Table 4). The level of differentiation did not change substantially when European samples were excluded from the analysis ($\Phi_{ST} = 0.857$, $P < 0.001$).

The haplotype network (Fig. 3B) displayed some evidence for either incomplete lineage sorting, gene flow, or both, as four samples were mapped outside their haplogroups. All four (one male and three females) were identified as either second-year or adult in age. One second-year male in the Beringia group (haplotype #7) and two adult females from Washington (haplotype #16 and #17) exhibited sequences more closely related to the Alaska, BC, Prince of Wales Island group, while one second year female sample in Washington (haplotype #20) showed a greater similarity to haplogroup 3b sequences from Western Ontario and Eastern North America. Based on observations associated with the Beringian sample and movements of juveniles tracked with satellite transmitters (Pearce and Petersen 2009), we conclude that these events are more likely dispersal and migratory events rather than incomplete lineage sorting (see Discussion).

Common Merganser winter samples

Among 193 North American and Eurasian wintering samples, we observed 66 haplotypes (not shown). In North America, 19 of these of these haplotypes were

identical to those observed among breeding area samples and occurred in 67% of winter samples. In a comparison of haplotype frequencies among three North American wintering areas (Alaska and Western and Eastern North America), we observed an overall significant level of population differentiation ($\Phi_{ST} = 0.370$, $P < 0.001$), but this was much reduced from the breeding area comparison ($\Phi_{ST} = 0.857$; Fig. 5B). In contrast to breeding data, there were more shared haplotypes among wintering regions (Fig. 5B) and more divergent lineages within areas.

In the 31 wintering samples from Denmark, 15 haplotypes were observed, and four of these matched breeding samples from Scotland. Four haplotypes were observed in the seven wintering samples from Vladivostok, Russia. Three samples were identical and matched haplotype #3 from the Western Aleutian Islands and Fairbanks (Table 2), and another two samples differed by a single base-pair from haplotype #4 observed in the Western Aleutian Islands (V47 in Table 2). The remaining two wintering samples from Russia (V50 and V51) were substantially different from haplotypes in Beringia (Table 2) and more closely related to European breeding samples (Fig. 3B). Except for the Russian samples, there were no other occurrences of shared haplotypes between North America and Eurasian wintering locations.

Based on exact haplotype matches and mtDNA spanning network analysis, we observed several wintering areas to be composed of multiple mtDNA haplogroups, but we also observed geographic variation in the pattern of heterogeneity (Fig. 6). Individuals from > 1 haplogroup were present in all winter areas except the Great Lakes, Eastern North America, and Denmark, although multiple breeding areas may

still be represented within these relatively homogeneous areas (see Discussion). In Western North America and the Intermountain West, proportions of different mtDNA haplogroups were similar for male and female samples. In heterogeneous areas, approximately half of all samples originated from mtDNA haplogroups other than the resident group, and in Western North America all four North American haplogroups were present. Most winter samples from Vladivostok, Russia were similar to those observed in Iceland and Poland by Hefti-Gautschi et al. (2008) since they contained an identical 3 base-pair indel (Table 2). This indel was not observed in any of the 31 winter samples from Denmark. After accounting for the shorter control region fragment sequenced in this study, 93% of winter samples from Denmark were identical to haplotypes from central and northern European areas identified by Hefti-Gautschi et al. (2008).

Discussion

Population structure of breeding areas

The Red-breasted Merganser presents a classic pattern of panmictic population structure within North America common to many species that have expanded their ranges to more northerly latitudes following the last glacial maximum in North America and Eurasia (Avise 2000, Milá et al. 2007). As a result, we were unable to reject either of two possible scenarios responsible for limited differentiation of Red-breasted Merganser mtDNA within North America: female-mediated gene flow or insufficient time since range expansion for site-faithful behavior (philopatry) to

structure populations genetically (reviewed in Pearce and Talbot 2006). Information from other independent markers, such as stable isotope, mark-recapture, or satellite telemetry are needed to assess levels of female philopatry and dispersal patterns in the Red-breasted Merganser (Boulet et al. 2006, Pearce et al. 2008). Correlated patterns of mtDNA nucleotide differences with geographic locale were noted between continental sampling areas, however, suggesting either limited long-distance gene flow or incomplete lineage sorting following a recent population expansion. Given the geographic distance between continents, the latter scenario seems more likely and was confirmed through a *post-hoc* analysis of North American and European breeding data using the 'Isolation with Migration' (IM) program (Nielsen and Wakeley 2001). Following a run of 8×10^6 steps (minimum ESS = 1,368) the peak of the posterior distribution for the migration rate (m) between North American and Western European samples was low (0.02), with confidence intervals that overlapped zero (95% HPD: 0.00–0.10), suggesting incomplete lineage sorting rather than gene flow.

In contrast to Red-breasted Mergansers, mtDNA from Common Mergansers revealed substantial population structure among all groups, suggesting limited female-mediated gene flow. This indirect evidence of female philopatry was found not only in the reciprocal monophyly among sampling regions, but also at finer scales. Among samples from single locales in Alaska, such as Fairbanks and the Togiak and Anchor rivers, we observed independent samples to have identical haplotypes, suggesting shared lineages as a result of long-term philopatry to individual river drainages. Despite the disappearance of Pleistocene barriers to dispersal that contributed to the

phylogeographic structure of other taxa (Smith et al. 2001, Milá et al. 2007, Pruett and Winker 2008), this has not resulted in obvious secondary contact among historically isolated groups of Common Mergansers. Only four samples–1 male and 3 females–yielded sequences from outside each monophyletic haplogroup (Fig. 3B). Two of these, one male and one female, were sampled in July and April, respectively, and were of subadult plumage. Based on the movements of sub-adult Common Mergansers marked with satellite transmitters (Pearce and Petersen 2009), we assume that these two outsider events are the result of dispersal in the male and pre-breeding movements by the female. The remaining two outsider events were both by females, one adult and one of unknown age. The adult was from Prince of Wales Island and sampled in October, while the unknown-aged female was sampled in March.

The haplotype network for Common Merganser mtDNA in North America suggests a complex pattern of population history. For example, the relationship of haplotypes in Beringia to those further south does not imply a simple post-Pleistocene, stepping-stone colonization pattern along the Pacific Coast to more northerly areas as glaciers retreated. Instead of an intermediate position for the Alaska, BC, and Prince of Wales Island haplogroup, this clade appears derived from the Beringian group and is placed intermediate between Washington and Beringia in the spanning network (Fig. 2B). Also, all samples from Eastern and Western Beringia are more closely related to North America than to Asia, which differs from New World–Old World patterns of several avian taxa with ranges that span the Bering Sea (Zink et al. 1995, 2006, Drovetski et al. 2004). However, such a split may occur farther west in the Russian Far

East as is suggested by the admixture of New World–Old World lineages among wintering birds near Vladivostok, Russia (Table 2, Fig. 6).

Patterns of differentiation in the Common Merganser with mtDNA appear to be supported by nuclear loci, but only between continents. Pearce et al. (In Review) found no evidence for population differentiation within North America with genotypic data from seven nuclear microsatellite loci, suggesting male-mediated gene flow. In contrast, many of these same loci were invariable or failed to yield a PCR product for European samples (J. Pearce, unpubl. data), suggesting similarly deep levels of divergence with mtDNA. Similar patterns of low nuclear DNA differentiation within Europe, with higher levels between Europe and Canada, were also observed by Hefti-Gautschi et al. (2008).

Population structure and nesting ecology

Contrasting patterns of genetic differentiation in Red-breasted Merganser and Common Merganser raise questions about the evolutionary and ecological constraints of nesting behavior for ground nesting and cavity nesting species. While the evolutionary timing of the Red-breasted Merganser and ground nesting behavior is unknown, both appear to have arisen from an ancestral group of cavity nesting *Mergus* species (Livezey 1995). Ground nesting behavior may have allowed for competitive avoidance by the Red-breasted Merganser with closely related cavity nesting waterfowl species and an opportunity to expand into more northern boreal forest and tundra habitats where cavities of adequate size are likely rare.

In the Common Merganser, female population structure appears maintained by natal site fidelity that likely confers a fitness advantage. Among cavity nesting species of waterfowl, Common Mergansers have the largest body size, and thus they may be limited to a smaller proportion of natural cavities than their smaller-bodied congeners. In contrast, smaller-bodied cavity nesting waterfowl may exhibit more inconsistent patterns of site fidelity as a mechanism to avoid competition for nest sites (see Pearce et al. 2008). Cavity nesting in the Common Merganser also raises the question of what nesting habitat existed historically in the North Pacific as Beringian haplotypes diverged from the Western and Eastern North American haplotypes. Both pollen and macrofossil data suggest that tree species (*Populus*, *Picea*, and *Pinus*) survived within Beringia during the last glacial maximum, c. 28,000–15,000 (Brubaker et al. 2005). However, little is known about the size and structure of these forests and whether they could have supported cavities suitable for nesting. Two records of Common Merganser broods from the Western and Central Aleutian Islands need further substantiation as the islands do not support tree cavities and breeding Red-breasted Mergansers are common (Gibson and Byrd 2007).

Migratory connectivity

For both species, we observed 'weak' migratory connectivity (*sensu* Webster et al. 2002) and admixture of breeding haplotypes on the wintering grounds, resulting in lower levels of population differentiation for winter than breeding areas. However, inferring admixture and connectivity between breeding and wintering areas is more

problematic in the Red-breasted Merganser due to limited population differentiation. In contrast, Common Mergansers appear to move across phylogeographic boundaries along the Pacific Coast similar to movements observed with satellite transmitters by Pearce and Petersen (2009). Such seasonal movements by females may facilitate male dispersal and gene flow if females pair on non-natal wintering grounds with resident males. For male Common Mergansers, population heterogeneity on wintering grounds likely results from both seasonal migration and dispersal among divergent breeding areas, and both of these behaviors were observed among molting Common Mergansers in Alaska (Pearce et al., In Review). Thus, the finding of a Beringian haplotype in Western North America during winter could mean that either this individual dispersed to a new breeding area or migrated south for winter. Additional band-recovery and DNA analysis of samples collected from adult males on breeding areas may help to quantify rates of dispersal and seasonal migration.

We observed some wintering areas, such as Western North America and Vladivostok, Russia, that were comprised of individuals with very different mtDNA lineages as these areas are adjacent to major phylogeographic breaks in this species. Although wintering areas such as the Great Lakes and Eastern North America appear homogeneous, they likely contain individuals from multiple breeding areas that may be differentiated on a lesser scale than in Western North America. Interestingly, none of the 31 Denmark winter samples contained the unique three base-pair indel despite the occurrence of this mutation in breeding birds in Iceland and Poland (see Hefti-Gautschi et al. 2008). Thus, there may also be geographic variation in migratory tendency and

limited dispersal by males among some breeding populations in Europe, a pattern also observed in band-recovery data across North America (Pearce et al. 2005).

We speculate that life history traits, such as nesting behavior and dispersal tendencies, may have played substantial roles in structuring populations genetically. However, more research is required using both genetic and non-genetic approaches, to quantify basic characteristics of nesting biology and movements of Red-breasted and Common mergansers. For Common Mergansers, breeding data suggest a high degree of female philopatry, but substantial movement during nonbreeding periods. Philopatry has often been viewed as a constraint, placing avian populations at risk if local habitat or forage is disturbed. However, our genetic data suggest that females roam during nonbreeding periods, which may facilitate dispersal if natal areas became unsatisfactory.

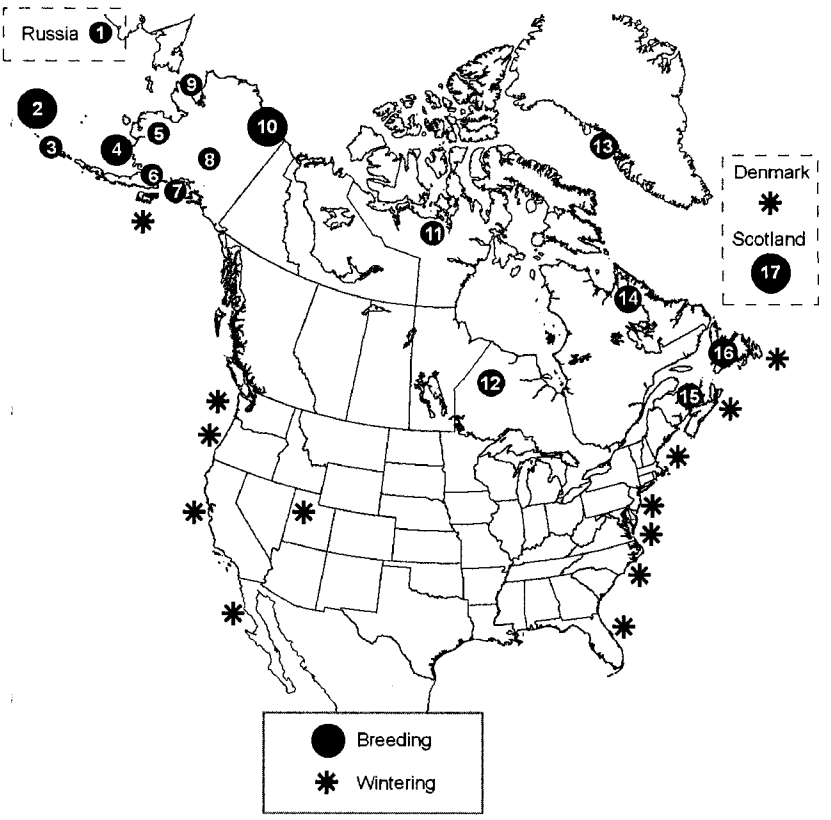

Figure 1. DNA sampling locales for Red-breasted Mergansers. Breeding samples are shown as circles proportional to sample size. Numbers within circles correspond to location names given in the Appendix. Approximate locations of winter samples are shown with an asterisk.

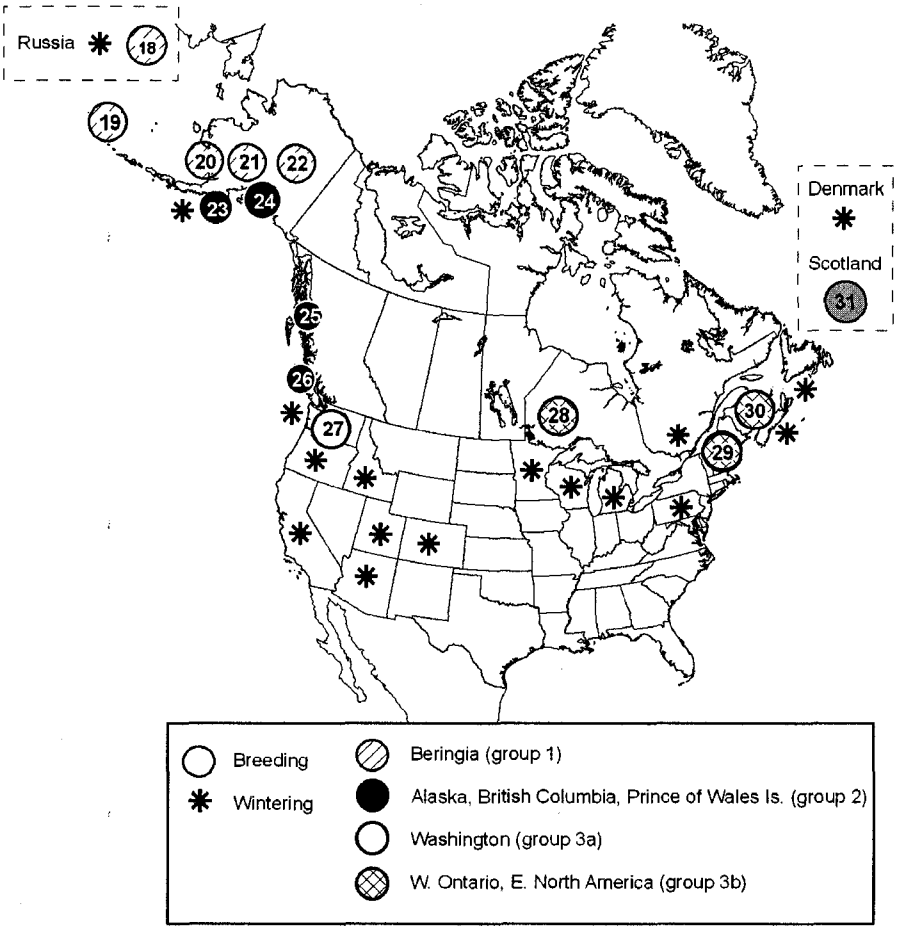

Figure 2. DNA sampling locales for Common Mergansers. Breeding samples are shown as circles proportional to sample size and are shaded according to mtDNA haplogroup. Numbers within circles correspond to location names given in the Appendix. Approximate locations of winter samples are shown with an asterisk.

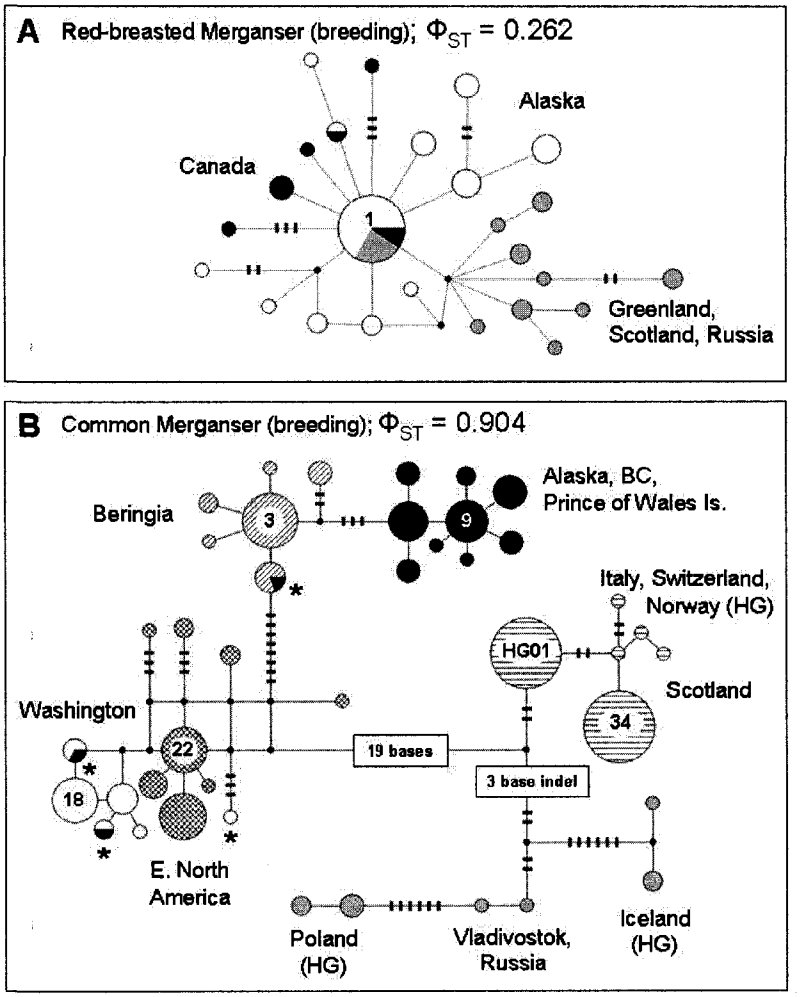

Figure 3. MtDNA haplotype networks for breeding Red-breasted and Common Mergansers and overall levels of population differentiation (Φ_{ST}). In both panels, numbers within circles correspond to common haplotypes. A single site substitution links each circle except where bars or text denote additional substitutions. Circles are proportional to the number of each haplotype observed. Small black dots are inferred intermediate haplotypes. In panel B, haplotypes labeled 'HG' are from Hefti-Gautschi et al. (2008, table 4). Winter samples from Vladivostok, Russia, that were more similar to European lineages are also included (see Results). Circles are color coded to match the major mtDNA haplogroups observed across North America as in Fig 2. Apparent dispersal or migratory events of four individuals are shown as asterisks.

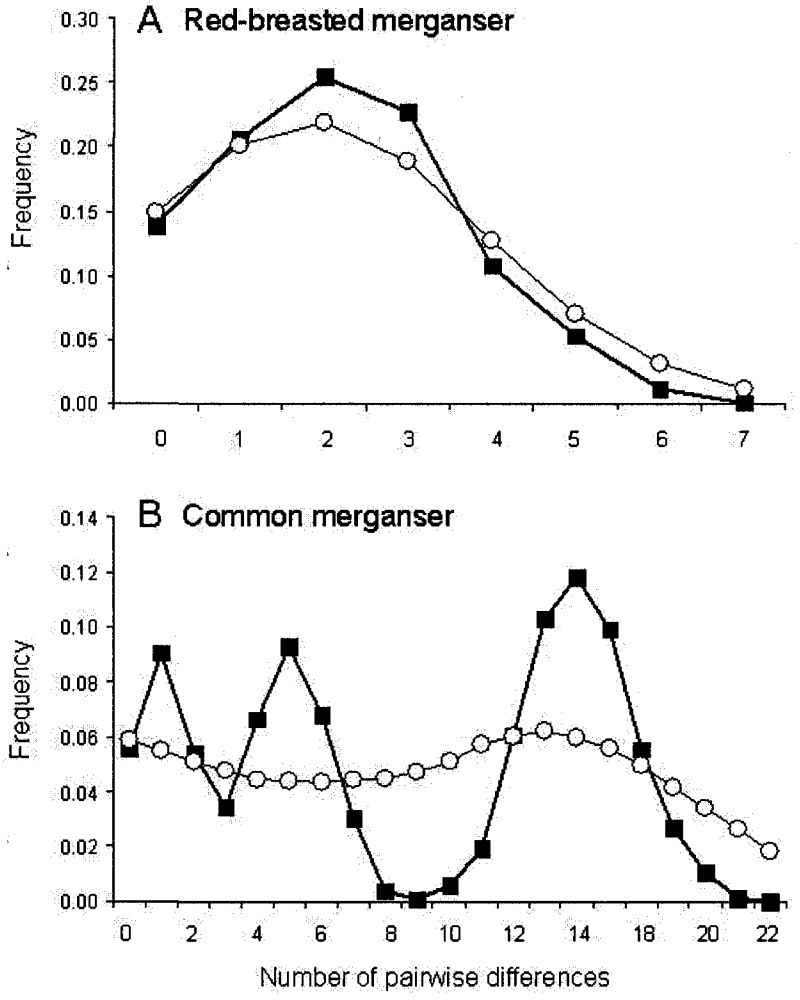

Figure 4. Mismatch distributions of mtDNA sequence data for North American breeding samples of (A) Red-breasted Mergansers and (B) Common Mergansers. Lines with black squares are the observed distributions, and lines with open circles are the expected distributions from simulations of demographic expansion.

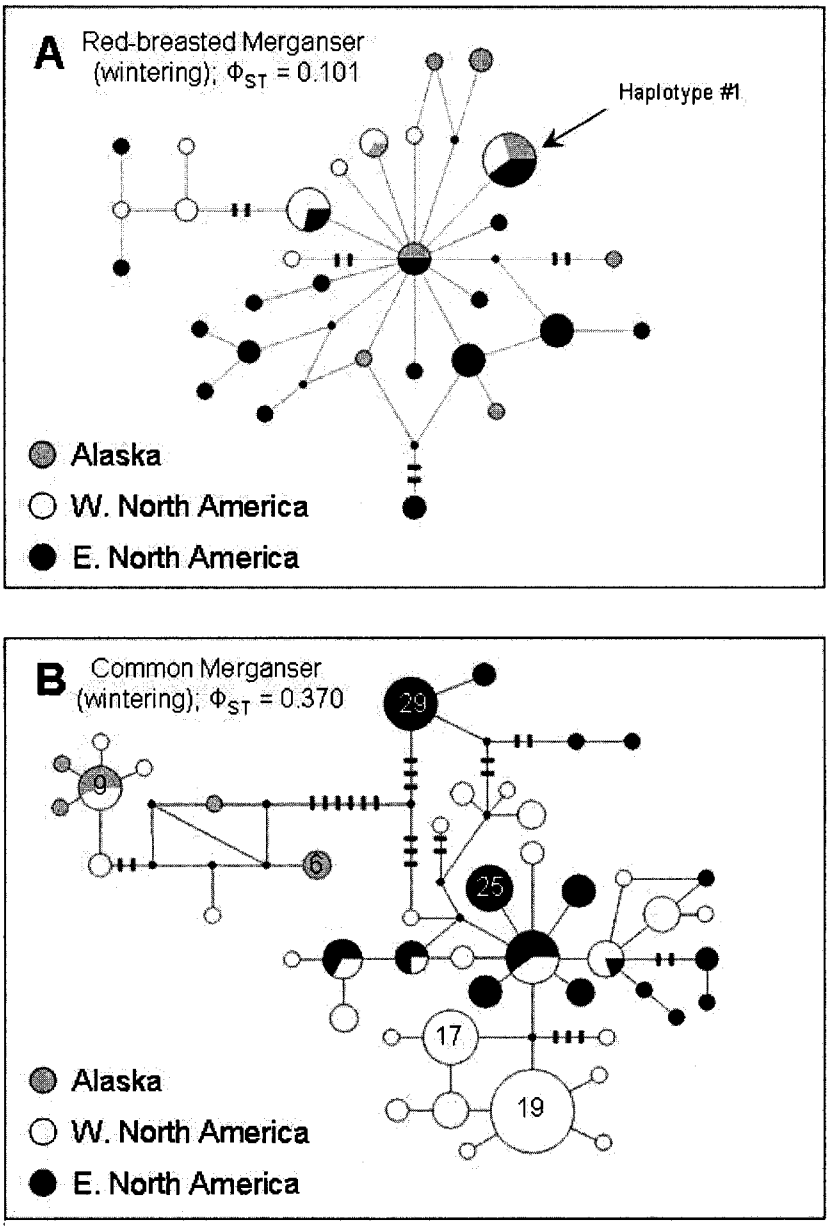

Figure 5. MtDNA haplotype networks for Red-breasted and Common Mergansers sampled on wintering areas and overall levels of population differentiation (Φ_{ST}). Circles are proportional to the number of each haplotype observed. Small black dots are inferred haplotypes. Numbers within circles correspond to common haplotypes listed in Tables 1 and 2.

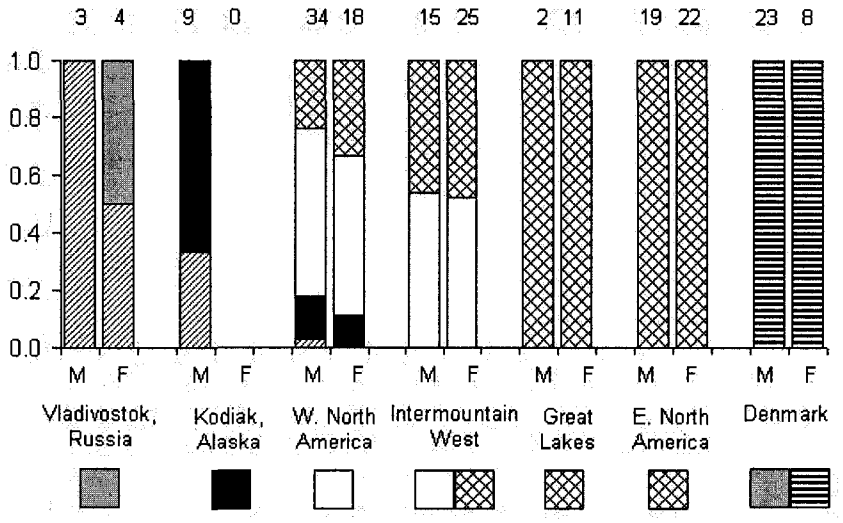

Figure 6. Frequency of mtDNA haplogroups among winter samples of male (M) and female (F) Common Mergansers across five North American and two Eurasian sites. Shading of bars corresponds to colors used in Figures 1 and 2B. Expected haplogroup composition of each wintering area, based on mtDNA of breeding samples, is shown in boxes below location names. Sample sizes appear above each bar.

Table 1. MtDNA control region haplotypes of Red-breasted Mergansers from North American and Eurasian breeding samples. Dots represent identical nucleotides to those shown in haplotype #1.

Haplotype		Sampling area and frequency		
		Alaska	Canada	Eurasian[a]
1	CCTACTCCCGACGCCTCAACAGAATTATC	14	2	5
2	.....CT.....G.....	3		
3	.....G.....	2		
4	.....AG.....	1		
5	..CG.....G.....	1		
6	.....G....C.....	2		
7	.....G.....	2		
8	T.....	3		
9	.....T.....A	4		
10	.....T.....	4		
11	.....TC.....C.	1		
12	.....C.....G..	1		
13	.....T.....		1	
14	.....A.....T.....		1	
15	.....T.....G.C...		1	
16	.T.....G.....		3	
17	...G.....A..C....			1
18	...GT.....T.T.....			2
19	...G.....G.....			2
20	T..G...T.....			2
21	...G.....T.....			1
22	...G...T.....			1
23	...G.....C....			2
24	...G.....A.....			1
25	...G.....CC...			1
Total		38	8	18

[a]Includes breeding samples from Greenland, Russia, and Scotland.

Table 2. MtDNA control region haplotypes of Common Mergansers, number (*n*), and location (Fig. 2) of each haplotype in North American and Eurasian breeding areas. Four haplotypes from wintering birds near Vladivostok, Russia (V47, 50, and 51) are also shown. Dots represent identical nucleotides to those shown in haplotype #1. Insertion and deletion events (indels) are shown as dashes.

Haplotype		*n*	Location
1	CACCACACTCAACCGCTTCCAACCTCCAACTTCCCCGCACACATCTTC-C---GCCCAGCAC	2	18, 19
2	..........T.....T	1	19
3	.....T	15	19, 22
4	.....T.....T.....T....T	1	19
5	.....C.....T	5	20
6	.....T.C.....T.....T	3	21
7	.....C.T.....C.....A.....T	8	20, 25, 26
8	.....C.T.....C..T.....A.....	6	24
9	.....C.T.....C..T.....A.....T	9	24
10	.....C.T.....C..T.....C....A.....T	2	23
11	.....C.T.....C..T.....C.A.....T	3	24
12	...T.....C.T.....C..T.....A.....T	1	25
13	.....C.T.....T....C.....A.....T	3	25
14	.....A.....C.T.....C..T.....A.....T	1	25
15	.....C.T.....C.....C.....A.....T	3	26
16	....G.....C.....C..G.T..T.T.....GTCC..C.A.....T.T..T.T	2	26, 27
17	....G.....C.....C....T....T.....GTCC..C.A.....T.T....T	2	26, 27
18	....G.....C.....C....T..T.T.....GTCC..C.A.....T.T....T	9	27
19	....G.....C.....C....T..T.T.....GTCC..C.A.....T.T..T.T	5	27
20	....G.....T...C.....TC....T....T.....G.CC..C.A.....T	1	27
21	....G....T.....C.....C....T..T.T.....GTCC..C.A.....T.T..T.T	1	27
22	....G.....C.....C....T....T.....G.CC..C.A.....T....T.T	10	28, 29, 30
23	....G.G...G..T...C.....T....T.....G.CC..C.A.....T.T..T.T	1	28
24	....G.....C.T....C....T....T.....G.CC..C.A.....T....T.T	1	28
25	....G.....C.....C...GT....T.....G.CC..C.A.....T....T.T	11	29, 30
26	....G.....C.....T....T.....G.CCT.C.AT....T.....T	2	30
27	....G.....C.....T....T....TG.CC..C.A.....T.T	2	28, 29
28	....G.....C.....C....TC...T.....G.CC..C.A.....T....T.T	4	29
29	....G.G.....T...C.....T....T.....G..C....A.....T.T	1	30
34	T.T.GT..C..GT.AA....GGT.CT.C.T.C.T..A.G....C.CC.A.....A.GT	2	31
36	T.T.GT..C..GT.AA.C..GGT.CT.C.T.C.T..A.G....C..CTA.....GA.GT	16	31
37	T.T.GT..C...T.AA.C..GGT.CT.C.T.C.T..ATG....C..C.A.....A.GT	2	31
V47	.....T....T	2	18
V50	TGT.GT..CT..T.A..C..G...CT.C.T.C.T.TA.....C..C.A.AACA....A.GT	1	18
V51	T.T.GT..CT..T.A..C..G...CT.C.T.C.T.TA.....C..C.A.AACA....A.GT	1	18
Total		139	

Table 3. Uncorrrected percent sequence divergence for Common Merganser mtDNA. Divergence values between the North American Common Merganser (*M. m. americanus*) and Eurasian Common Merganser or Goosander (*M. m. merganser*) are shown below the diagonal, and within-group divergence is shown along the diagonal.

	Beringia	Alaska, British Columbia, and Prince of Wales Is.	Washington, W. Ontario, and E. North America	Scotland and Denmark (*M. m. merganser*)*
Beringia	0.23–1.15			
Alaska, British Columbia, and Prince of Wales Is.	1.15–1.83	0.23–0.69		
Washington, W. Ontario, and E. North America	2.52–3.90	2.29–4.36	0.46–2.29	
Scotland and Denmark (*M. m. merganser*)	5.50–6.42	5.50–7.11	5.28–7.11	0.23 –1.38

*Samples of wintering birds from Denmark included in the analysis.

Table 4. Pairwise Φ_{ST} among Common Merganser breeding samples across North America in comparison to European samples from Scotland and Denmark.

	Alaska, British Columbia, and Prince of Wales Is.	Washington	W. Ontario	E. North America	Scotland and Denmark
Beringia	0.752*	0.918*	0.881*	0.858*	0.938*
Alaska, British Columbia, and Prince of Wales Is.		0.918*	0.887*	0.871*	0.939*
Washington			0.679*	0.642*	0.941*
W. Ontario				0.052*	0.921*
E. North America					0.918*

*$P < 0.001$

Literature Cited

Anderson, M. G., J. M. Rhymer, and F. C. Rowher. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. Pages 365–395 *in* Ecology and Management of Breeding Waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Avise, J. C. 2000. Phylogeography: The history and formation of species. Harvard University Press, Cambridge.

Avise, J. C., R. T. Alisauskas, W. S. Nelson, and C. D. Ankney. 1992. Matriarchal population genetic structure in an avian species with female natal philopatry. Evolution 46:1084–1096.

Bandelt, H. J., P. Forster, and A. Röhl. 1999. Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16:37–48.

Boulet, M., and D. R. Norris. 2006. The past and present of migratory connectivity. Ornithological Monographs 61:1–13.

Boulet, M., H. L. Gibbs, and K. Hobson. 2006. Integrated analysis of genetic, stable isotope, and banding data reveal migratory connectivity and flyways in the Northern Yellow Warbler (*Dendroica petechia*; *aestiva* group). Ornithological Monographs 61:29–78.

Brubaker, L. B., P. M. Anderson, M. E. Edwards, and A. V. Lozhkin. 2005. Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. Journal of Biogeography 32:833–848.

Drovetski, S. V., R. M. Zink, S. Rohwer, I. V. Fadeev, E. V. Nesterov, I. Karagodin, E. A. Koblik, and Y. A. Rad'kin. 2004. Complex biogeographic history of a Holarctic passerine. Proceedings of the Royal Society of London B 271:545–551.

Excoffier, L., G. Laval, and S. Schneider. 2005. ARLEQUIN version 3.1: An integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1:47–50.

Gibson, D. D., and G. V. Byrd. 2007. Birds of the Aleutian Islands, Alaska. Series in Ornithology, No. 1. Nuttall Ornithological Club and American Ornithologists' Union, Washington D.C.

Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

Hefti-Gautschi, B., M. Pfunder, L. Jenni, V. Keller, and H. Ellegren. 2008. Identification of conservation units in the European *Mergus merganser* based on nuclear and mitochondrial DNA markers. Conservation Genetics 9: in press.

Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. Nature 405:907–913.

Livezey, B. C. 1995. Phylogeny and evolutionary ecology of modern seaducks (Anatidae: Mergini). Condor 97:233–255.

Mallory, M., and K. Metz. 1999. Common Merganser (*Mergus merganser*). *In* The birds of North America, No. 442 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Medrano, J. F., E. Aasen, and J. Sharrow. 1990. DNA extraction from nucleated red blood cells. Biotechniques 8:43.

Milá, B., T. B. Smith, and R. K. Wayne. 2007. Postglacial population expansion drives the evolution of long-distance migration in a songbird. Evolution 60:2403–2409.

Nielsen, R., and J. Wakeley. 2001. Distinguishing migration from isolation: A Markov chain Monte Carlo approach. Genetics 158:885–896.

Pearce, J. M. 2006. Minding the gap: Frequency of indels in mtDNA control region sequence data and influence on population genetic analyses. Molecular Ecology 15: 333–341.

Pearce, J. M. 2007. Philopatry: A return to origins. Auk 124:1085–1087.

Pearce, J. M., J. A. Reed, and P. L. Flint. 2005. Geographic variation in survival and migratory tendency among North American Common Mergansers. Journal of Field Ornithology 76:109–118.

Pearce, J. M., and S. L. Talbot. 2006. Demography, genetics, and the value of mixed messages. Condor 108:474–479.

Pearce, J. M., P. Blums, and M. Lindberg. 2008. Site fidelity is an inconsistent determinant in population structure in the Hooded Merganser (*Lophodytes cucullatus*): Evidence from mark-recapture, genetic and comparative data. Auk 125:711–722.

Pearce, J. M., and M. R. Petersen. 2009. Post-fledging movements of juvenile Common Mergansers (*Mergus merganser*) in Alaska as inferred by satellite telemetry. Waterbirds, in press.

Pearce, J. M., D. Zwiefelhofer, and N. Maryanski. Mechanisms of population heterogeneity of molting Common Mergansers on Kodiak Island, Alaska: Implications for genetic assessments of migratory connectivity. Condor, In Review.

Posada, D., and K. A. Crandall. 1998. Modeltest: Testing the model of DNA substitution. Bioinformatics 14:817–818.

Pruett, C. L., and K. Winker. 2008. Evidence for cryptic northern refugia among high and temperate-latitude species in Beringia: A response to Stewart and Dalén (2008). Climate Change 86:23–27.

Rogers, A. R., and H. C. Harpending. 1992. Population growth makes waves in the distribution of pairwise genetic differences. Molecular Biology and Evolution 9:552–569.

Smith, C. T., R. J. Nelson, C. C. Wood, and B. F. Koop. 2001. Glacial biogeography of North American coho salmon (*Onchorhynchus kisutch*). Molecular Ecology 10:2775–2785.

Tamura, K., and M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 10:512–526.

Tamura, K., J. Dudley, M. Nei, and S. Kumar. 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. Molecular Biology and Evolution 24:1596–1599.

Titman, R. D. 1999. Red-breasted Merganser (*Mergus serrator*). *In* The birds of North America, No. 443. (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Villesen, P. 2007. FaBox: An online toolbox for FASTA sequences. Molecular Ecology Resources 7:965–968.

Webster, M. S., P. P. Marra, S. M Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: Unraveling migratory connectivity. Trends in Ecology and Evolution 17:76–83.

Webster, M. S., and P. P. Marra. 2005. The importance of understanding migratory connectivity and seasonal interactions. Pages 199–209 *in* Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Zink, R. M., S. Rohwer, A. A. Andreev, and D. L. Dittman. 1995. Trans-Beringia comparisons of mitochondrial DNA differentiation in birds. Condor 97:639–649.

Zink, R. M., A. Pavlova, S. Rohwer, and S. V. Drovetski. 2006. Barn Swallows before barns: population histories and intercontinental colonization. Proceedings of the Royal Society of London B 273:1245–1251.

Appendix. List of sampling sites, season of collection, sample source, size (*n*), and geographic coordinates for Red-breasted Merganser and Common Mergansers included in this study. Specific sampling site names and coordinates were unavailable for many wintering areas in US states and Canadian provinces and are left blank.

Sampling sites	State or province, Country	Sample source[a]	*n*	Latitude	Longitude
Red-breasted Merganser					
Breeding samples					
Yamalo-Nenetski (1)	Russia	UWBM 59478, 59567	2	68.01	68.36
Attu Is., Aleutian Is. (2)	Alaska, USA	KGM831, KGM839, UAMX 4610, 4611, 4626, 4627, 4631, 4632, 4637, 4638, 4643	11	52.50	–173.10
Amchitka Is., Aleutian Is. (3)	Alaska, USA	Nest	1	51.30	–179.00
Good News River (4)	Alaska, USA	Tissue	5	59.07	–161.35
Johnson River (5)	Alaska, USA	Tissue	3	60.47	–161.45
Brooks River (6)	Alaska, USA	Feather	1	58.33	–155.47
Skilak Lake (7)	Alaska, USA	Tissue	2	60.28	–150.28
Fairbanks (8)	Alaska, USA	Tissue	4	64.49	–147.44
Cape Espenberg (9)	Alaska, USA	Nest	1	66.34	–163.44
Ivishak River (10)	Alaska, USA	Tissue	9	68.42	–146.53
Karrak Lake (11)	Alaska, USA	Nest	1	67.14	–100.14
Big Trout Lake (12)	Ontario, Canada	Tissue	1	53.45	–90.00
Greenland (13)	Greenland	Nest	1	68.10	–52.50
George River (14)	Quebec, Canada	Tissue	2	58.30	–65.50
Kouchibouguac Natl. Park (15)	New Brunswick, Canada	Nest	4	46.50	–64.58
New Foundland (16)	New Foundland, Canada	Tissue	1	49.00	–57.50
Montrose	Scotland	Tissue	15	56.42	2.28

Appendix, *continued*

Wintering samples					
Kodiak Is.	Alaska, USA	Tissue	12	57.45	–152.23
	Washington, USA	Wing	1	47.30	–120.00
	Oregon, USA	Wing	1	44.00	–120.35
	California, USA	Wing	1	36.50	–120.00
Bahia de San Quintin	Baja, Mexico	Wing	4	30.24	–115.58
	Utah, USA	Wing	9		
	New Foundland, Canada	Wing	3		
	Nova Scotia, Canada	Wing	3		
	Maine, USA	Wing	3		
	Massachusetts USA	Wing	3		
	New Jersey, USA	Wing	6		
	Rhode Is., USA	Wing	3		
	Connecticut, USA	Wing	1		
	Virginia, USA	Wing	6		
	North Carolina, USA	Wing	1		
	Florida, USA	Wing	3		
Limfjorden	Denmark	Wing	15	57.00	9.00
Common Merganser					
Breeding samples					
Magadan (18)	Russia	UWBM 43819	1	59.32	150.52
Shemya Is., Aleutian Is. (19)[b]	Alaska, USA	Tissue (2), UAM 24117, 24299, 24306	5	52.42	–174.06
Togiak River (20)	Alaska, USA	Tissue	6	59.02	–160.24
Novi River (21)	Alaska, USA	Tissue	2	62.56	–155.32
Nowitna R. (21)	Alaska, USA	Tissue	1	62.56	–155.32
Fairbanks (22)	Alaska, USA	Tissue (8), nest (3)	11	64.49	–147.44
Delta Junction (22)	Alaska, USA	Tissue	1	64.04	–145.42

Appendix, *continued*

Dalton Highway (22)	Alaska, USA	UAM 21870	1	68.00	–149.59
Anchor River (23)	Alaska, USA	Nest	6	59.46	–151.49
Kenai River (23)	Alaska, USA	Tissue	3	60.28	–150.28
Hope (23)	Alaska, USA	Tissue	2	60.53	–149.37
Kodiak Is. (23)	Alaska, USA	Nest	2	57.45	–152.23
Cordova (24)	Alaska, USA	Tissue	6	60.32	–145.45
Prince of Wales Is. (25)	Alaska, USA	Wing	9	57.32	–134.30
Port Alberni (26)	British Columbia, Canada	Tissue	4	49.14	–124.48
Gold R. (26)	British Columbia, Canada	Tissue	5	49.41	–126.07
Columbia R. (27)	Washington, USA	Tissue	18	47.30	–120.10
Western Ontario (28)	Ontario, Canada	Tissue	8	50.40	–94.25
Vermont (29)	Vermont, USA	Tissue	11	44.00	–72.50
Aziscohos Lake (29)	Maine, USA	Nest	1	45.00	–71.00
Restigouche River (30)	New Brunswick, Canada	Tissue	12	48.04	–66.20
Aberdeen (31)	Scotland	Tissue	15	57.08	2.05
Wintering samples					
Vladivostok	Russia	Wing	7	43.13	131.41
Limfjorden	Denmark	Wing	31	57.00	9.00
Kodiak Is.	Alaska, USA	Tissue	9	57.45	–152.23
	Washington, USA	Wing	10		
	Oregon, USA	Wing	33		
	California, USA	Wing	9		
	Arizona, USA	Wing	6		
	Utah, USA	Wing	17		
	Idaho, USA	Wing	7		
	Colorado, USA	Wing	10		
	Minnesota, USA	Wing	2		

Appendix, *continued*

Michigan, USA	Wing	6
Wisconsin, USA	Wing	5
Pennsylvania, USA	Wing	22
Quebec, Canada	Wing	6
New Foundland, Canada	Wing	10
Nova Scotia, Canada	Wing	3

[a]Numbers in parentheses refers to the number of samples of the following tissue types: 'wing' = samples collected by the U.S., Canadian, and Danish Parts Collection Surveys; 'feather' = sampled from salvaged or captured bird; 'nest' = salvaged nesting material (i.e., egg-shell membranes and feathers). Vouchered museum specimens are indicated as follows: UWBM = University of Washington Burke Museum; KGM, UAM, and UAMX = University of Alaska Museum. All other samples are currently held at the USGS, Alaska Science Center.

[b]Considered as breeding samples in this paper, but Common Mergansers in the Aleutian Island are likely migrants as breeding records are unsubstantiated (Gibson and Byrd 2007).

CHAPTER 4. Mechanisms of Population Heterogeneity among Molting Common Mergansers on Kodiak Island, Alaska: Implications for Genetic Assessments of Migratory Connectivity[4]

Abstract

Quantifying genetic heterogeneity within nonbreeding aggregations can inform our understanding of patterns of site fidelity, migratory connectivity, and gene flow between breeding and nonbreeding areas. However, characterizing mechanisms that contribute to heterogeneity, such as seasonal migration and dispersal, is required before accurate assessments of site fidelity and migratory connectivity can be made. We studied nonbreeding groups of Common Mergansers (*Mergus merganser*) molting on Kodiak Island, Alaska, from 2005–2007 using banding data to assess site fidelity, mitochondrial (mt) DNA and morphological measures to determine population affiliation, and nuclear microsatellite genotypes to assess the occurrence of seasonal migration and dispersal. Using mtDNA haplotype baseline information from well-defined mtDNA haplogroups across North America, we were able to assign individuals to natal regions and document population genetic heterogeneity within and among molting groups. Band-recovery and mtDNA data suggest that both seasonal migration and dispersal contribute to admixed groups of males molting on Kodiak Island. A lack

[4]Pearce, J.M., D. Zweifelhofer, and N. Maryanski. Mechanisms of Population Heterogeneity among Molting Common Mergansers on Kodiak Island, Alaska: Implications for Genetic Assessments of Migratory Connectivity. Prepared for submission to *The Condor*.

of genetic differentiation across North America for nuclear DNA suggests that natal area assignments may be uninformative as male dispersal leads to admixture on breeding and molting areas. Our results suggest that inferring levels of migratory connectivity and assignments of mtDNA group membership can be substantially biased as a result of sex-biased dispersal. Thus, multiple and independent data types are required to account for such behaviors before accurate assessments of migratory connectivity can be made.

Introduction

The migration of birds to nonbreeding areas for staging, molting, or wintering is a common phenomenon. Nonbreeding areas may be located far from the breeding grounds and offer sources of nutrition needed for subsequent migrations and reproduction as well as protection from predators and weather (Alcock 1993). Enhancements to fitness gained in one portion of the annual cycle may be carried over to subsequent life history stages (Marra et al. 1998, Weitkamp and Neely 2002). Quantifying these various effects is useful for interpreting population dynamics and trends of animal aggregations at a specific point in the annual cycle, but requires an understanding of migratory connectivity between breeding and nonbreeding areas (Webster et al. 2002). That is, do most individuals from one breeding area move to the same nonbreeding area, or are nonbreeding areas heterogeneous, composed of individuals from multiple breeding populations? Within group heterogeneity is important to quantify because if each group present in the admixture has different

demographic qualities, then averaging across these different groups may bias estimates of life history parameters. Furthermore, understanding the mechanisms that contribute to population heterogeneity within groups of animals, such as dispersal or seasonal migration, is a critical first step for delineating populations and assessing the degree of migratory connectivity. Such mechanisms may vary by sex, age, as well as across broad temporal and spatial scales (Avise et al. 1992, Fedy et al. 2008).

Aggregations of animals at nonbreeding areas are often more amenable to study than on breeding areas, when individuals of many species are widely dispersed at lower densities. Nonbreeding waterfowl (family Anatidae) are particularly easy to capture and study during the flightless molting period. Whereas many avian species maintain their flight capability throughout prolonged molting periods (Langston and Rohwer 1996, Voelker and Rohwer 1998), most species of waterfowl shed their flight feathers simultaneously, necessitating a 20–50 day period of complete flightlessness (Hohman et al. 1992). The capture and marking of molting waterfowl has been useful for quantifying annual survival rates (Flint et al. 2000), movement and site fidelity during molt (Bollinger and Derksen 1996, Flint et al. 2004, Nicolai et al. 2005), examining disease transmission (Hollmén et al. 2003), and determining the energetic requirements of molt (Guillemette et al. 2007).

The degree of population heterogeneity within nonbreeding groups of waterfowl has not often been examined. Previous studies have used various methods to assess population heterogeneity, such as mark-recapture (Bollinger and Derksen 1996, Dau et al. 2000), genetic methods (Bjorndal and Bolten 2008), and morphological criteria

(Pearce et al. 2000). Fewer studies have combined inferences from multiple data sources to assess heterogeneity and also infer mechanisms that contribute to population admixture (Bjorndal and Bolten 2008, Fedy et al. 2008). This combination of data types is useful when single markers (genetic or mark-recapture data) lack sufficient resolution to characterize within-group variation, but also when populations are highly diverged for a single data type (Pearce and Talbot 2006, Pearce et al. 2008).

The Common Merganser (*Mergus merganser*) is a large sea duck with a Holarctic distribution. Mark-recapture and satellite telemetry data suggest that male Common Mergansers undertake long-distance molt migrations, whereas females molt near natal areas (Little and Furness 1985, Pearce and Petersen 2009). Thus, molting flocks of Common Mergansers may be composed of individuals from multiple natal areas, but this may differ between the sexes. Analyses of mitochondrial (mt) DNA variation across the North American range of the Common Merganser by Pearce et al. (In Review), revealed substantial population differentiation across multiple breeding areas in North America. This divergent population structure suggests that the natal origins of birds encountered on nonbreeding areas can be deduced via an analysis of mtDNA group membership. Indeed, Pearce et al. (In Review) observed that Common Mergansers sampled during winter in the Pacific Northwest (Washington, Oregon, and California) originated from all four mtDNA haplogroups in North America. Similar genetic 'mixed stocks' were also observed among wintering Common Mergansers in Europe (Hefti-Gautschi et al. 2008).

Although the determination of natal origins of nonbreeding Common Mergansers on the basis of mtDNA haplotype appears straightforward, such assignments may not reflect current breeding area use by an individual because of dispersal as well as seasonal migration (Fig. 1). Unlike other birds, male waterfowl are typically the dispersing sex, thus contributing to gene flow among populations. Juvenile males are thought to disperse away from natal areas after fledging (Anderson et al. 1992). However, not all male movement may result in gene flow and may instead reflect seasonal migration between natal and nonbreeding areas. Thus, different types of data aside from mtDNA, such as band recoveries and nuclear DNA, are needed to assess the frequency of both seasonal migration and dispersal as behaviors that contribute to heterogeneity within a nonbreeding aggregation.

We used mtDNA group membership to determine whether molting Common Mergansers on Kodiak Island, Alaska were derived from multiple natal origins and examined whether group membership varied temporally and spatially across the island. Secondly, we evaluated the association between body size and mtDNA haplogroup divisions to determine if structural size of molting birds could be useful for population differentiation in the field. Lastly, we used genotypic data from seven nuclear microsatellite DNA and band recovery data as an independent method to infer relative frequencies of seasonal migration and dispersal hypotheses to explain any population heterogeneity observed within flocks. For this final objective, we hypothesized that if males undertake molt migrations strictly on a seasonal basis (i.e., returning to natal genetic origins after the molt), then similar levels of breeding population structure

should exist for bi-parentally inherited nuclear DNA as observed with maternally inherited mtDNA. However, if males are dispersing prior to the molt, then nuclear DNA among breeding areas should show little if any population structure in comparison to mtDNA.

Methods

Study area and data collection

To understand the distribution of molting Common Mergansers across Kodiak Island, we mapped fresh and marine water locations of Kodiak Island where > 50 molting birds were observed from 1994–2007 (Fig. 2). From these locations, we selected five areas that were within our logistical constraints to conduct captures and DNA sampling. These locations included the freshwater Frazer and Karluk lakes and marine areas of Uyak, East Arm Uganik, and Terror bays (Fig. 2). We captured and sampled flightless male Common Mergansers from 2005–2007, including Karluk Lake (12–21 July 2005, 11–13 July 2006, and 20–22 July 2007), Frazer Lake (20 July 2007), and the three marine areas (12–14 July 2007). Mergansers were captured using small boats to herd flocks of flightless birds into an onshore net enclosure. Near-shore boat surveys were conducted each year on Karluk Lake before and after captures to estimate the total number of molting males present. Capture and sampling procedures were approved by the Institutional Animal Care and Use Committee at the U.S. Geological Survey (USGS), Alaska Science Center and the University of Alaska Fairbanks.

We classified all captured birds as males based on plumage characteristics, cloacal exams, and a molecular sexing technique (below). We marked each bird with a metal leg band and collected standard morphological measures to assess structural size and stage of molt. These measures included exposed culmen, total tarsus, mid-wing (distal end of the radius to the proximal end of the ulna measured on the dorsal surface), ninth primary length, and body mass. Following determination of mtDNA group membership (below), we used box plots to compare morphological measures (culmen, total tarsus, and mid-wing) of birds with haplotypes from each of three Pacific Coast mtDNA haplogroups (1, 2, and 3a) identified by Pearce et al. (In Review). We also used discriminant function analysis in SPSS version 14.0 to examine if combinations of structural measures could accurately classify individuals to their mtDNA group of origin. Body mass and ninth primary were not included in these analyses, because these are more likely to be based on individual body condition and timing of molt rather than population characteristics. For mtDNA group assignment of molting Common Mergansers, we collected 2–3 small ($\leq$ 2 cm) emerging feather quills from the secondary wing covert tracts of captured birds.

DNA extraction, sex verification, and mtDNA sequencing

We extracted DNA from all samples following methods described in Pearce et al. (2004) and verified that all sampled birds were males using the P8 and P2 polymerase chain reaction primers developed by Griffiths et al. (1998) as described in Pearce et al. (In Review). To determine mtDNA group membership, we amplified and sequenced a

425 base pair fragment of the control region (domain I) of mtDNA using primers MMCR LF and MMCR LR designed for the European Common Merganser (Hefti-Gautschi et al. 2008) and methods identical to those described in Pearce et al. (2008). We aligned all sequences with the program AlignIR version 2.0 (LI-COR, Inc.) and organized multiple sequences into unique haplotypes using the COLLAPSE function of the FaBox software (Villesen 2007). We deposited all mtDNA haplotypes into GenBank (accession numbers FJ190980–FJ191172).

Population genetic and statistical analyses

Significant population differentiation was noted among four mtDNA haplogroups by Pearce et al. (In Review). However, because not all breeding areas within the geographic range of group 3a and 3b were sampled, we restrict our assignment of individuals to the three main mtDNA groups (1, 2, and 3a/3b). We refer to each group as the 'genetic' or 'natal' origin of each bird. Haplogroups 1–3 are reciprocally monophyletic and defined by 3–8 fixed nucleotide differences (Fig. 2). For mtDNA group assignment, we compared the sequence of each molting Common Merganser to the breeding haplotypes observed by Pearce et al. (In Review) using COLLAPSE. Group assignment of novel haplotypes was determined through a comparison to the breeding haplotypes using a Neighbor-joining tree in MEGA version 4 (Tamura et al. 2007). Trees were constructed using 10,000 bootstrap replicates and a Tamura-Nei model of nucleotide evolution as identified by Pearce et al. (In Review).

We tested for annual and spatial differences in the number of haplotypes from each group using exact tests of population differentiation via *F*-statistics (F_{ST}) and AMOVA with the program ARELQUIN version 3.0 (Excoffier et al. 2005). Two sets of analyses were performed: (1) annual samples from Karluk Lake (2005–2007) and (2) site-specific samples from all additional areas where birds were captured in 2007, plus a composite sample from Karluk Lake that contained the frequencies of all haplotypes observed from 2005–2007, excluding recaptured individuals. F_{ST} values were computed using conventional *F*-statistics from haplotype frequencies and significance was assessed by comparison to values generated from 10,000 random permutations. ARLEQUIN was also used to compute haplotype (*h*) diversity for each sampling location.

Nuclear DNA from breeding areas

To examine if patterns of molt migration to Kodiak Island resulted from seasonal migration, dispersal prior to molt, or both, we obtained nuclear microsatellite genotypes from seven loci for 140 breeding samples collected across North America. Specific sampling locations of breeding areas are described in Pearce et al. (In Review), but briefly, we used 45 samples from Western Ontario and Eastern North America (Vermont, Maine, and New Brunswick), 20 from Washington state, 54 from south central Alaska, British Columbia (BC), and Prince of Wales Island, and 21 from Beringia (western and interior Alaska). Samples included feathers or egg shell

membranes (n = 14), blood samples (n = 28), and tissues (n = 98). All samples were collected from females or hatch-year birds on the breeding grounds.

From an initial screening of 66 microsatellite loci, we selected seven for analysis: APH04 and APH08 (Maak et al. 2003), CRG (A. Baker, pers. comm. F 5'-GTAGGCAAAGCAAGTCTGAAGTT-3', and R 5' -GCAACCACCAGCAGTCACTACAA-3'), Hhiμ5 (Buccholz et al. 1998), MM01 and MM02 (Gautschi and Koller 2005), and HrU2 (Primmer et al. 1995). Gautschi and Koller (2005) isolated nine loci for the European Common Merganser, but all except MM01 and MM02 were monomorphic or yielded no PCR product, likely because of the relatively deep divergence (5–7% sequence divergence) between these two continental groups (Pearce et al., In Review). PCR amplification of all nuclear loci during screening and data collection involved identical reagent cocktails as described in Pearce et al. (2004) except that all were amplified with the same PCR temperature profile (94°C for 2 min followed by 40 cycles of 94°C for 2 min, 50°C for 1 min and 72°C for 1 min) using an MJ Research PTC-200 thermal cycler. PCR products were visualized on 6% polyacrylamide gels using a LI-COR 4200 DNA sequencer (LI-COR, Inc.). Genotypes were scored according to allele size based on an initial comparison to an M13 DNA sequence ladder and then to samples established as size standards that were run on each subsequent gel.

For each microsatellite locus we calculated allelic frequencies, number of alleles per locus (A), and observed (H_o) and expected (H_e) heterozygosities using ARLEQUIN. We used GENEPOP (Raymond and Rousset 1995) to conduct exact

probability tests for deviations from Hardy-Weinberg equilibrium in each sampling area following the method of Guo and Thompson (1992). We further assessed deviations from Hardy-Weinberg by estimating Wright's inbreeding coefficient, F_{IS}, across all loci for each sampling area using Program FSTAT version 2.9.3 (Goudet 1995). Positive values of F_{IS} indicate heterozygotic deficiency, a signal of inbreeding or population admixture (i.e., Wahlund effect), whereas negative values indicate heterozygotic excess.

Results

Mark-recapture of males

From 2005–2007, we captured and banded 176 molting Common Merganser males at Karluk Lake (Table 1). Only four of these marked birds were recaptured in subsequent years even though our capture effort averaged 41% of all birds molting on the lake (Table 1). MtDNA haplotypes of three of the four recaptured birds aligned most closely with group 2 (Alaska, British Columbia, and Prince of Wales Island) and the fourth with group 1 (Beringia). Three males banded during molt on Kodiak Island (2 in 2005 and 1 in 2007) were subsequently recovered by hunters in January: two in Washington state in 2006 and a third in California in 2008 (Table 1). MtDNA from one of these birds aligned most closely with group 3 (Western and Eastern North America). Additionally, a male captured during molt at Karluk Lake in 2005 had been originally banded in April 2004 in south-central Alaska near Seward (60°05'N, 149°25'W).

Population membership: mtDNA and morphology

We obtained mtDNA sequence data for 190 samples across Kodiak Island (Table 2). Seventy-seven percent of samples were identical to one of the 29 North American breeding haplotypes observed by Pearce et al. (In Review), with the remainder yielding 25 new haplotypes. Novel haplotypes were observed in each year at Karluk Lake and across all sites except Uyak Bay. Haplotypic diversities were high across all areas, even in Uyak Bay where few samples ($n = 7$) were collected (Table 2).

Our analysis of temporal variation in mtDNA group membership at Karluk Lake from 2005–2007 suggested no difference in the proportions of each of the three groups ($F_{ST} = 0.002$, $P = 0.451$), with group 2 haplotypes (Alaska, British Columbia, and Prince of Wales Island) being the most common (Fig. 3B). Greater variation in the frequency of group 2 haplotypes was observed in our analysis of spatial variation in membership across all five sampling sites (Fig. 3C). In this analysis, group membership varied significantly across sites ($F_{ST} = 0.071$, $P = 0.001$) as a result of differences between 2 of 10 pairwise comparisons (Karluk Lake vs. Terror Bay and Terror Bay vs. Uganik Bay). A greater proportion of group 3 haplotypes (Western and Eastern North America) were present in Uyak and Terror bays. We observed no difference in the means and distribution of morphological measurements of 115 molting males across Kodiak Island (Fig. 4) and a discriminant function analysis, based largely on the first of two functions (eigenvalue 0.071, percent of variance explained = 98.3%), correctly classified only 33% of original cases to the three mtDNA groups. These

results suggested that mtDNA group membership of males cannot be distinguished in the field with linear measures of culmen, tarsus, and mid-wing.

Nuclear microsatellite variation among breeding areas

Across the 140 Common Merganser breeding samples analyzed for seven loci, average variation was 2–10 alleles, but was consistent for each locus across all sampling areas (Table 3). Significant deviations from Hardy-Weinberg proportions ($P < 0.05$) were detected in 4 of the 28 area-by-locus combinations. No consistent pattern of deviation was noted across all sampling areas, except for the MM02 locus, which exhibited significant heterozygote deficiencies in all areas but Western North America (Table 3). Exact tests of Hardy-Weinberg equilibrium showed significant values ($P < 0.05$) in 2 of 84 comparisons, but pairs of loci in these two tests were not the same (data not shown). None of the four sampling areas exhibited significantly large F_{IS} values, which is an alternate indicator of heterozygotic deficiency (Table 3). The overall estimate of F_{ST} across broadly distributed breeding areas was low and non-significant ($F_{ST} = 0.002$, $P = 0.73$), suggesting gene flow.

Discussion

Common merganser females sampled on their breeding areas exhibit a high degree of population structure for mtDNA (Pearce et al., In Review), but not for bi-parentally inherited nuclear microsatellite loci as observed by our microsatellite analysis. A similar low level of nuclear DNA differentiation was also noted among European

Common Mergansers (Hefti-Gautschi et al. 2008). This lack of concordance between mitochondrial and nuclear DNA is expected for a species with female philopatry and male dispersal and is typical of waterfowl (Scribner et al. 2001, Avise 2004). However, such pronounced discordance between different classes of molecular markers is not always observed, and reasons for this include historic and contemporary population and range expansion and female-mediated gene flow (Avise et al. 1992, Peters and Omland 2007, Pearce et al. 2008). In contrast to breeding areas, nonbreeding groups of Common Mergansers (molting and wintering) appear, based on mtDNA, to be composed of individuals from multiple breeding areas, a result of both dispersal and seasonal migration. The implication of male-mediated nuclear gene flow for nonbreeding areas is that population genetic heterogeneity at Kodiak Island cannot be attributed to direct connectivity between Kodiak Island and distant natal areas, such as for individuals with group 1 and 3a haplotypes. Instead, nuclear DNA suggests that male dispersal is ongoing within and among breeding areas of North America, while limited band-recovery data suggest long-distance, seasonal migration to Kodiak Island. Thus, males on breeding areas are likely to be as equally heterogeneous as observed on molting areas (Fig. 1). As a result, inferring levels of migratory connectivity (*sensu* Webster et al. 2002) is problematic in this species and likely to be in other taxa with sex-biased dispersal tendencies.

While we cannot estimate the proportions of each movement type (dispersal and migration) used by male Common Mergansers, our data suggest that dispersal is more common than seasonal migration. Nuclear DNA is undifferentiated among broadly

sampled breeding areas, suggesting gene flow. Additionally, Pearce et al. (In Review) observed that 42% of both male and female winter samples collected in Washington, Oregon, and California ($n = 54$) were outsider events. Because these individuals were recovered during winter, a time when species of waterfowl are believed to form breeding pairs, we assume that these represent both migratory and dispersal events to the Western and Eastern North American haplogroup. Only limited evidence from band recovery and mtDNA suggests that some males at Kodiak are seasonal, long-distance migrants and not dispersing across mtDNA boundaries before molting in Alaska. Three birds banded on Kodiak Island during molt were recovered in January in Washington and California (Table 1). A DNA sample from one of these recoveries was most closely related to the Western and Eastern North American haplogroup (Fig. 2), suggesting this bird migrated to Kodiak for molt before returning to its natal area to winter. Long-distance molt migration has also been documented among European Common Mergansers with banding data (Little and Furness 1985).

The long-distance migrations implied by our band recovery data could also be interpreted as annual northward migration to Alaska breeding and molting areas, followed by a return migration to more southerly wintering areas. Band recovery information for Common Mergansers from elsewhere in North America suggests a seasonal migration for some areas (Pearce et al. 2005), but it is unknown what proportion of Alaska breeding birds undertake such a migration. Common Mergansers are observed throughout ice-free interior rivers and coastal marine areas of Alaska during winter. A larger band-recovery data set or deployment of satellite transmitters

to track the annual movements of individual males would improve our understanding of migratory behaviors. Additionally, an assessment of mtDNA group affiliation of pre-breeding males across North America would yield information about the proportion of immigrant haplotypes within each breeding group.

Our three-year mark-recapture analysis at Karluk Lake suggests low molt site fidelity among male Common Mergansers. Interestingly, the small number of recaptures we did observe were of birds with group 1 and 2 haplotypes (Table 1), rather than the more geographically distant group 3. Despite this absence of site fidelity, the proportional representation of mtDNA groups was maintained across years at Karluk Lake (Fig. 2B). Given the low level of site fidelity we observed, one would expect greater annual variation in mtDNA group proportions at Karluk Lake. Additional years of sampling across Kodiak Island are needed to clarify if the consistent mtDNA group proportions observed over three years at Karluk Lake is due to sampling bias or other factors. For example, in aggregations of nonbreeding Green Turtles (*Chelonia mydas*), Bjorndal and Bolten (2008) found little annual variation in population membership, as inferred by mtDNA haplotype, in a series of four years, but substantial variation when the entire 10-year data set was considered. These authors identified factors such as breeding colony productivity to contribute substantially to the annual variation of different mtDNA groups in nonbreeding aggregations. Within-year temporal variation at each site may also occur across Kodiak Island. We sampled molting birds in early July each year at Karluk Lake, but flightless Common Mergansers are observed on the lake until early September (D. Zwiefelhofer, unpubl. data), and different proportions of

the three groups may be present toward the end of the molting period. However, we observed no difference in the average lengths of new ninth-primary wing feathers among 115 birds from each of the three mtDNA groups (Kruskal Wallis $X^2 = 0.291$, df = 2, $P = 0.86$; data not shown), suggesting similar timing of molt among all birds.

Molting female Common Mergansers in Scotland showed greater levels of site fidelity than we observed for males, but some switching of sites was also observed (Hatton and Marquiss 2004). Patterns of molt site fidelity among sea ducks are highly variable with respect to measurement scale and methodology (Flint et al. 2000, 2004, Iverson et al. 2004, Mehl et al. 2004, Phillips et al. 2006). We do not conclude that low site fidelity results in heterogeneity within molting flocks of Common Mergansers, but instead view the two behaviors as decoupled. For example, Steller's Eiders showed high levels (> 95%) of molt site fidelity to specific beaches in Alaska (Flint et al. 2000), but little connectivity between molting and breeding areas (Dau et al. 2000). Similarly, molting Black Brant (*Branta bernicla*) from multiple nesting colonies throughout Alaska and Canada exhibited high site fidelity (0.95%) to specific lakes on the North Slope of Alaska (Bollinger and Derksen 1996). Thus, as has been argued previously (Pearce and Talbot 2006, Pearce et al. 2008), site fidelity is an inconsistent measure of within-group population composition or demographic independence among groups.

We found no morphological differences among males after assigning birds to haplogroups based on mtDNA (Fig. 3, Table 4). Thus, field morphological measures cannot be used to reliably identify genetic origins as is possible with mtDNA, although intra-specific variation in morphology has been useful in other mixed stock scenarios

for identifying the presence of different groups (Wennevik et al. 2008). Common mergansers are a generalist piscine predator, consuming a wide variety of aquatic prey and are known to shift to alternate species when primary prey become less abundant (Weise et al. 2008). Different migration strategies among males likely take them to a variety of habitats, each with their own prey composition. Thus, it seems unlikely for bill morphology to become specialized to a specific region (i.e., be correlated with mtDNA group). In a phylogenetic analysis of structural measures, Livezey (1995) noted that among sea ducks, cavity-nesting species exhibit the largest sexual size dimorphism. Thus, cavity-nesting females appear constrained to small body size, whereas males are not as they play no role in nest selection or incubation. We predict that female Common Mergansers may also show no variation in bill morphology due to prey switching (Weise et al. 2008), but may exhibit structural size differences as female philopatry, evidenced by mtDNA population structure, to specific cavity-nesting habitats might lead to ecological specialization and regional differences in body size. Additional information is needed on both the nesting habits and structural size of female Common Mergansers across North America to assess these predictions.

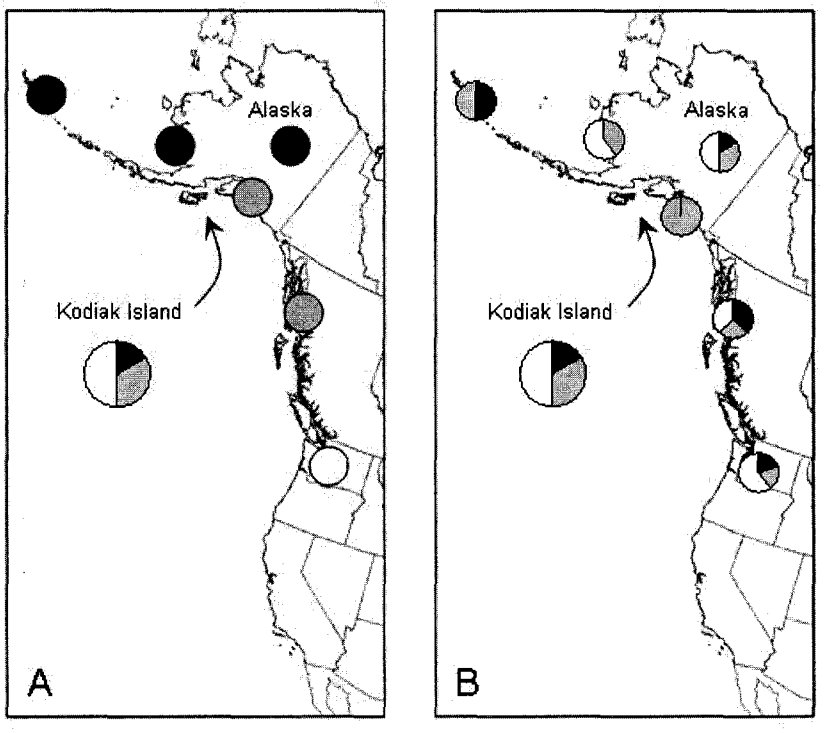

Figure 1. Possible mechanisms that contribute to population heterogeneity of molting Common Mergansers at Kodiak Island, Alaska. Evidence for both scenarios (seasonal migration in A and dispersal in B) was found using a combination of data types. In A, colored circles represent population structure based on mtDNA analysis of breeding females (see Pearce et al., In Review). If molting males seasonally migrate to Kodiak Island, then mtDNA accurately assesses population group membership (pie chart) and levels of migratory connectivity between breeding and nonbreeding areas. In B, pie charts demonstrate how male dispersal (inferred from nuclear microsatellite DNA) likely results in mtDNA heterogeneity in males at each breeding area similar to molting groups at Kodiak Island, which complicates assessments of group membership and migratory connectivity. Maps modified from Pearce et al. (In Review). Pie charts are for illustration purposes only and do not reflect actual mtDNA composition in each area.

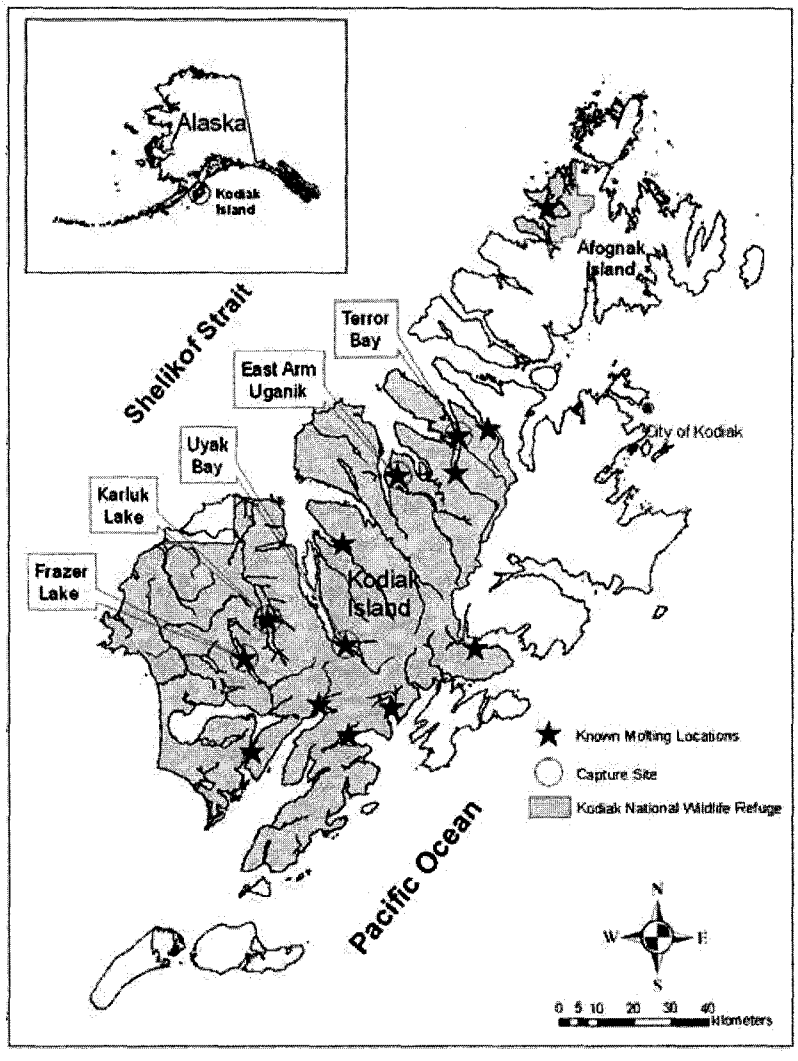

Figure 2. Molting locations of Common Mergansers on Kodiak Island, Alaska, and capture and sampling sites visited in 2005–2007.

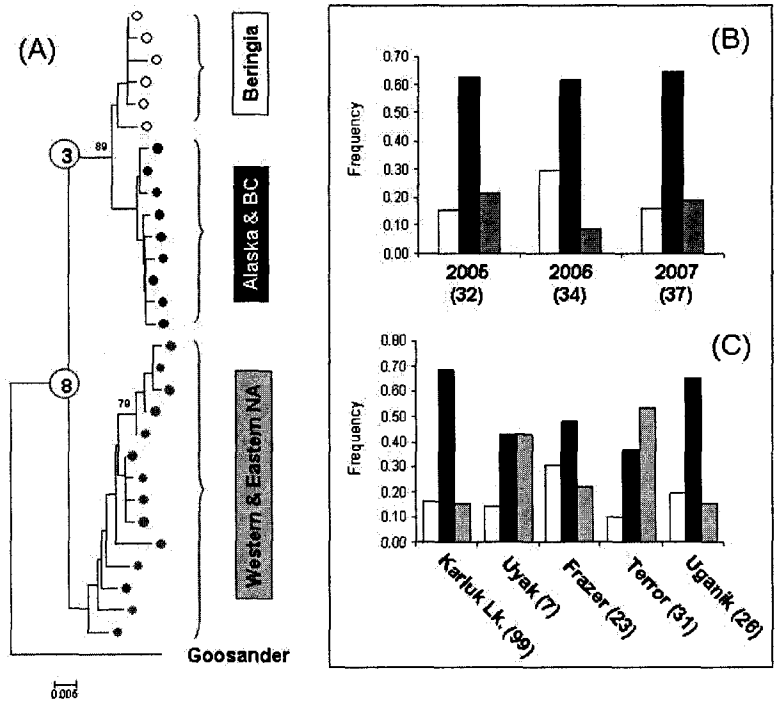

Figure 3. Assignment of molting Common Mergansers to one of three mtDNA haplogroups based on (A) phylogenetic relationships of mtDNA haplotypes from Common Merganser breeding areas across North America described Pearce et al. (In Review). Homologous mtDNA sequence of European Common Merganser was used as an outgroup. Assignment of molting male Common Mergansers was to one of three haplogroups: (1) Beringia, (2) Alaska, British Columbia, and Prince of Wales Island (Alaska/BC/POW), or (3) Western and Eastern North American (NA). Numbers at nodes indicate total fixed nucleotide differences between groups. Bootstrap values > 70% are also shown. (B) Temporal variation in mtDNA groups at Karluk Lake from 2005–2007. (C) Spatial variation in mtDNA groups across Kodiak Island, Alaska in 2007 compared to composite sample from Karluk Lake. Sample sizes of mtDNA are shown in parentheses and color of bars in B and C and correspond to each of the three major mtDNA groups in A.

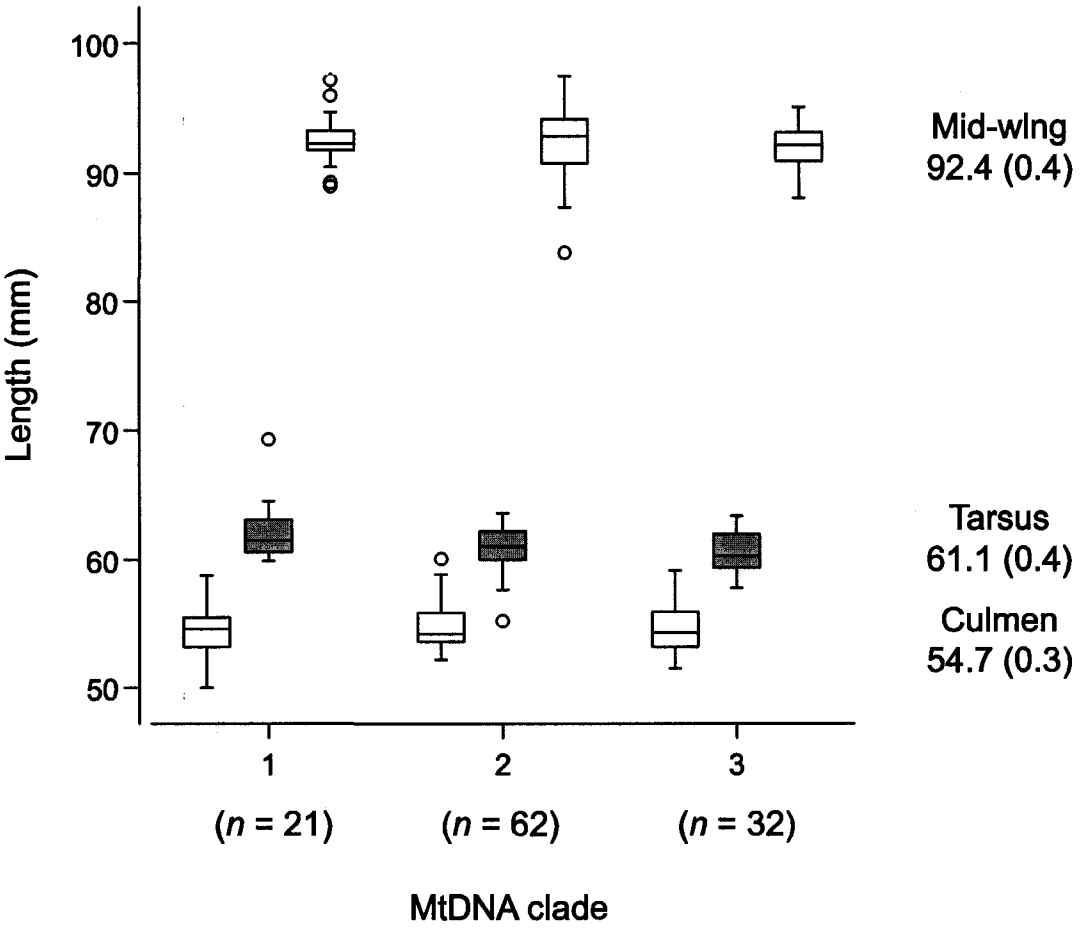

Figure 4. Boxplots of morphological variables of male Common Mergansers across the three major mtDNA haplogroups in North America. Center line in boxplots represents the median value and 50% of observed values lie within the boxes. Outlier values are shown as small circles. Sample sizes are shown along the x-axis, and mean values (± SE) are shown at right.

Table 1. Number of molting male Common Mergansers captured on Karluk Lake, Kodiak Island, Alaska, and number of band recoveries following initial banding.

Year	Number captured	Molting birds on Karluk Lake[a]	Band-recaptures (mtDNA group membership)	Band-recoveries[b]
2005	85	142	-	2 (Washington)
2006	52	148	2 (group 2)	
2007	39	141	2 (group 1 and 2)	1 (California)

[a]Based on shoreline boat surveys conducted before and after the time of molt captures.

[b]Number and state of band-recoveries.

Table 2. Sample size (N), number of unique (A) and novel haplotypes, and haplotypic diversity (*h*) among molting male Common Mergansers sampled at Kodiak Island, Alaska.

Location	*n*	A	Novel	*h*
Karluk Lake				
2005	32	15	3	0.87 ± 0.05
2006	34	10	2	0.81 ± 0.05
2007	37	17	3	0.79 ± 0.07
Composite[a]	99	27	-	0.81 ± 0.04
Frazer Lake	23	8	1	0.78 ± 0.08
Uganik Bay	26	13	2	0.90 ± 0.04
Terror Bay	31	19	5	0.95 ± 0.03
Uyak Bay	7	6	0	0.95 ± 0.10

[a]All Karluk Lake samples excluding recaptures.

Table 3. Microsatellite allele variation and observed and expected heterozygosity in Common Merganser breeding areas. 'A' is the number of alleles observed (*$P < 0.001$).

	Beringia ($n = 21$)		Alaska, BC, and Prince of Wales Is. ($n = 54$)		Washington ($n = 20$)		Western Ontario and Eastern NA ($n = 45$)	
Locus	A	H_o/H_e	A	H_o/H_e	A	H_o/H_e	A	H_o/H_e
Hhiμ5	2	0.29/0.49	2	0.46/0.45	2	0.30/0.47	2	0.42/0.38
MM02	7	0.38/0.73*	8	0.42/0.73*	6	0.53/0.76	7	0.19/0.69*
APH04	9	0.75/0.85	10	0.81/0.82	8	0.74/0.78	9	0.86/0.81
MM01	6	0.62/0.61	9	0.57/0.62	7	0.45/0.57	9	0.60/0.80*
APH08	2	0.69/0.55	3	0.46/0.52	3	0.75/0.60	3	0.67/0.56
CRG	3	0.43/0.42	2	0.42/0.37	2	0.30/0.43	4	0.43/0.39
HrU2	3	0.35/0.35	3	0.20/0.18	3	0.30/0.38	4	0.26/0.25
F_{IS}		0.103		0.124		0.097		0.085

Literature Cited

Alcock, J. 1993. Animal Behavior: An Evolutionary Approach. Fifth edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Anderson, M. G., J. M. Rhymer, and F. C. Rowher. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. *In* Ecology and management of breeding waterfowl, pp. 365–395. (B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Avise, J. C. 2004. Molecular markers, natural history, and evolution. Second edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Avise, J. C., R. T. Alisauskas, W. S. Nelson, and C. D. Ankney. 1992. Matriarchal population genetic structure in an avian species with female natal philopatry. Evolution 46:1084–1096.

Bjorndal, K. A., and A. B. Bolten. 2008. Annual variation in sources contributions to a mixed stock: implications for quantifying connectivity. Molecular Ecology 17:2185–2193.

Bollinger, K. S., and D. V. Derksen. 1996. Demographic characteristics of molting Black Brant at Teshekpuk Lake, Alaska. Journal of Field Ornithology 67:141–158.

Buchholz, W. G., J. M. Pearce, B. J. Pierson, and K. T. Scribner. 1998. Dinucleotide repeat polymorphisms in waterfowl (family Anatidae): characterization of a sex-linked (Z-specific) and 14 bi-parentally inherited loci. Journal of Animal Genetics 29:323–325.

Dau, C. P., P. L. Flint, and M. R. Petersen. 2000. Distribution of recoveries of Steller's Eiders banded on the lower Alaska Peninsula, Alaska. Journal of Field Ornithology 71:541–548.

Excoffier, L., G. Laval, and S. Schneider. 2005. ARLEQUIN version 3.1: an integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1:47–50.

Fedy, B. C., K. Martin, C. Ritland, and J. Young. 2008. Genetic and ecological data provide incongruent interpretation of population structure and dispersal in naturally subdivided populations of White-tailed Ptarmigan (*Lagopus leucura*). Molecular Ecology 17:1905–1917.

Flint, P. L., M. R. Petersen, C. P. Dau, J. E. Hines, and J. D. Nichols. 2000. Annual survival and site fidelity of Steller's Eiders molting along the Alaska Peninsula. Journal of Wildlife Management 64:261–268.

Flint, P. L., D. L. Lacroix, J. A. Reed, and R. B. Lanctot. 2004. Movements of flightless Long-tailed Ducks during wing molt. Waterbirds 27:35–40.

Gautschi, B., and B. Koller. 2005. Polymorphic microsatellite markers for the Goosander (*Mergus merganser*). Molecular Ecology Resources 5:133–134.

Goudet, J. 1995. FSTAT version 1.2: a computer program to calculate *F*-statistics. Journal of Heredity 86:485–486.

Guo, S. W., and E. A. Thompson. 1992. Performing the exact test of Hardy-Weinberg proportion for multiple alleles. Biometrics 48:361–372.

Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

Guillemette, M., D. Pelletier, J. M. Grandbois, and P. J. Butler. 2007. Flightlessness and the energetic cost of wing molt in a large sea duck. Ecology 88:2936–2945.

Hefti-Gautschi, B., M. Pfunder, L. Jenni, V. Keller, and H. Ellegren. 2008. Identification of conservation units in the European *Mergus merganser* based on nuclear and mitochondrial DNA markers. Conservation Genetics 9: in press.

Hatton, P. L., and M. Marquiss. 2004. The origins of molting Goosanders on the Eden Estuary. Ringing and Migration 22:70–74.

Hohman, W. L., C. D. Ankney, and D. H. Gordon. 1992. Ecology and management of postbreeding waterfowl. *In* Ecology and management of breeding waterfowl, pp. 129–189. (B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Hollmén, T. E., J. C. Franson, P. L. Flint, J. B. Grand, R. B. Lanctot, D. E. Docherty, and H. M. Wilson. 2003. An adenovirus linked to mortality and diseases in Long-tailed Ducks (*Clangula hyemalis*) in Alaska. Avian Diseases 47:1434–1440.

Iverson, S. A., D. Esler, and D. J. Rizzolo. 2004. Winter philopatry of Harlequin Ducks in Prince William Sound, Alaska. Condor 106:711–715.

Langston, N. E., and S. Rohwer. 1996. Molt-breeding tradeoffs in albatrosses: life history implications for big birds. Oikos 76:498–510.

Little, B., and R. W. Furness. 1985. Long distance molt migration by British Goosanders, *Mergus merganser*. Ringing and Migration 6:77–82.

Livezey, B. C. 1995. Phylogeny and evolutionary ecology of modern seaducks (Anatidae: Mergini). Condor 97:233–255.

Maak, S., K. Wimmers, S. Weigend, and K. Neumann. 2003. Isolation and characterization of 18 microsatellites in the Peking Duck (*Anas platyrhynchos*) and their application in other waterfowl species. Molecular Ecology Resources 3:224–227.

Marra, P. P., K. A. Hobson, and T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:2040–2042.

Mehl, K. R., R. T. Alisauskas, K. A. Hobson, and D. K. Kellett. 2004. To winter east or west? Heterogeneity in winter philopatry in a central-arctic population of King Eiders. Condor 106:241–251.

Nicolai, C. A., P. L. Flint, and M. L. Wege. 2005. Annual survival and site fidelity of Northern Pintails banded on the Yukon-Kuskokwim Delta, Alaska. Journal of Wildlife Management 69:1202–1210.

Pearce, J. M., S. L. Talbot, B. J. Pierson, K. T. Scribner, D. L. Dickson, and A. Mosbech. 2004. Lack of spatial genetic structure among nesting and wintering King Eiders. Condor 106:229–240.

Pearce, J. M., J. A. Reed, and P. L. Flint. 2005. Geographic variation in survival and migratory tendency among North American Common Mergansers. Journal of Field Ornithology 76:109–216.

Pearce, J. M., and S. L. Talbot. 2006. Demography, genetics and the value of mixed messages. Condor 108:474–479.

Pearce, J. M., P. Blums, and M. Lindberg. 2008. Site fidelity is an inconsistent determinant of population structure in the Hooded Merganser (*Lophodytes cucullatus*): evidence from genetic, mark-recapture, and comparative data. Auk 125:711–722.

Pearce, J. M., and M. R. Petersen. 2009. Postfledging movements of juvenile Common Mergansers (*Mergus merganser*) in Alaska as inferred by satellite telemetry. Waterbirds, in press.

Pearce, J. M., K. G. McCracken, T. K. Christensen, and Y. N. Zhuravlev. Population genetic structure and migratory connectivity of breeding and wintering Red-breasted and Common Mergansers. Auk, In Review.

Peters, J. L., and K. E. Omland. 2007. Population structure and mitochondrial polyphyly in North American Gadwalls (*Anas strepera*). Auk 124:444–462.

Phillips, L. M., A. N. Powell, and E. A. Rexstad. 2006. Large-scale movements and habitat characteristics of King Eiders throughout the nonbreeding period. Condor 108:887–900.

Primmer, C. R., A. P. Møller, and H. Ellegren. 1995. Resolving genetic relationships with microsatellite markers: a parentage testing system for the swallow *Hirundo rustica*. Molecular Ecology 4:493–498.

Raymond, M., and F. Rousset. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenism. Journal of Heredity 86:248–249.

Scribner, K. T., M. R. Petersen, R. L. Fields, S. L. Talbot, J. M. Pearce, and R. K. Chesser. 2001. Sex-biased gene flow in Spectacled Eiders (Anatidae): Inferences from molecular markers with contrasting modes of inheritance. Evolution 55:2105–2115.

Tamura, K., J. Dudley, M. Nei, and S. Kumar. 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. Molecular Biology and Evolution 24:1596–1599.

Villesen, P. 2007. FaBox: an online toolbox for FASTA sequences. Molecular Ecology Resources 7:965–968.

Voelker, G., and S. Rohwer. 1998. Contrasts in scheduling of molt and migration in Eastern and Western Warbling-vireos. Auk 115:142–155.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology and Evolution 17:76–83.

Weitkamp, L., and K. Neely. 2002. Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. Canadian Journal of Fisheries and Aquatic Science 59:1100–1115.

Wennevik, V., K. E. Jørstad, G. Dahle, and S-. E. Fevolden. 2008. Mixed stock analysis and the power of different classes of molecular markers in discriminating coastal and oceanic Atlantic cod (*Gadus morhua* L.) on the Lofoten spawning grounds, Northern Norway. Hydrobiologia 606:7–25.

Wiese, F. K., J. K. Parrish, C. T. Thompson, and C. Maranto. 2008. Ecosystem-based management of predator-prey relationships: piscivorous birds and salmonids. Ecological Applications 18:681–700.

General Conclusions

Natal site fidelity, or philopatry, is thought not only to structure populations, but also to indicate that by returning to a given location, a migratory individual's fitness is somehow enhanced (Greenwood 1980). The research presented in this dissertation focused less on the potential benefits of site fidelity to individual fitness and instead on appropriate definitions and quantifications of site faithful behavior. There may indeed be advantages to site faithful behavior in general, but the genetic implications of philopatry (i.e., population structure) should not automatically be assumed, as has become more frequent in the scientific literature (Chapter 1, Pearce 2007). This is important as management and conservation strategies are often focused on a local area during a single time period of the year, such as the breeding season. If the probability of site fidelity is low, then enhancement scenarios to that area, such as reintroductions, predator removal, or habitat improvements may do little to alter the current status and future trend of individuals in that area.

In Chapter 1, and throughout much of the dissertation, I argue that not all types of site fidelity are equal, a high degree of site fidelity is not a universal proxy for population structure and delineation, and accurately quantifying levels of site fidelity must be undertaken with a battery of independent data sets. Additionally, I discussed how the use of different data sets can generate what appear to be contradictory conclusions or 'mixed messages'. Such discordance between data types should be viewed as a powerful tool to infer across multiple temporal and behavioral layers of information that describe the contemporary state of animal populations. By combining

genetic and mark-recapture data through a comparative approach, the list of possible causes for any mixed messages can be better understood. Such causes might include non-neutrality and mutational patterns of some of the DNA loci under study, demographic instability over longer time scales, previously undetected dispersal, or the inadequate use of dispersal models with mark-recapture or genetic data. Lastly, I argued that to understand the implications of winter site fidelity, information is needed on the migratory patterns and connectivity between winter and breeding sites.

Chapter 2 moved beyond simple commentary with an empirical example of a 'mixed message' in the Hooded Merganser. Using a long-term, live mark-recapture data set, I estimated that adult breeding site fidelity of females was high (>90%). Such high estimates are expected to result in limited female gene flow and population genetic structure (Anderson et al. 1992) and have been used to justify the designation of demographically independent units (see Chapter 1). However, using standard and Bayesian analysis of mitochondrial (mt) DNA sequence data from across the North American breeding range of the Hooded Merganser, I found evidence of female-mediated gene flow. Such dispersal events were also evident in band-recovery data and were higher in comparison to another cavity nesting species of waterfowl, the Wood Duck. The use of these various data sets demonstrated the different temporal and spatial scales of mark-recapture and genetic data, as well as how one data set can be used to inform predictions and results with another data type. For example, Pearce et al. (2005) observed geographic variation in survival and migratory tendency among

Common Mergansers and suggested that such variation had implications for the population genetic structure of the species.

Therefore, in Chapter 3, I used mtDNA sequence data to examine this prediction of population structure based on band-recovery data. I also examined general patterns of dispersal and migratory connectivity between breeding and wintering areas of the Common and Red-breasted merganser. These two species differ not only in their general breeding and wintering distributions across North America and the Old World, but also with respect to nesting ecology: the Red-breasted Merganser nests on the ground while the Common Merganser is primarily a cavity nester (Mallory and Metz 1999, Titman 1999). Continental patterns of Common Merganser mtDNA were found to be reflective of the historical band-recovery data. Three well-defined haplogroups were observed across North America, suggesting long-term female philopatry. In contrast, mtDNA characteristics of Red-breasted Mergansers suggested either incomplete lineage sorting since a recent population expansion, gene flow, or both. The Red-breasted Merganser is thus a good candidate for evaluation with additional independent data sets to help inform the population genetic results.

An analysis of DNA samples collected in winter across North American and other Eurasian locations found that levels of population structure in both Red-breasted and Common Mergansers were lower than those with samples collected during the breeding season. Evidence for mixing of individuals from multiple and often highly genetically divergent breeding areas was most obvious in the Common Merganser in the Pacific Northwest, where near equal proportions of the four different mtDNA

haplogroups were present for both males and females. This analysis suggested that although females appear to be philopatric to breeding areas, they wander during nonbreeding periods and this may facilitate male-mediated but not female-mediated gene flow among breeding areas. It is likely that some low level of female gene flow is taking place among what appear to be monophyletic haplogroups, but additional sampling of breeding female Common Mergansers across their range is needed to determine the frequency of this behavior. I suggest that the evolution of ground nesting in the Red-breasted Merganser is a derived trait that has allowed this species to rapidly expand its breeding distribution northward post-Pleistocene into areas that cannot support cavity nesting species of similar or larger body size, such as the Common Merganser. Genetic data suggest that female philopatry has been a long-term behavior among Common Mergansers, possibly as a result of limited large cavities available and the need for local knowledge through site familiarity to consistently breed. On the other hand, Red-breasted Mergansers can be highly mobile and disperse widely across the landscape as a ground nesting species. However, more work is needed on actual rates of natal site fidelity by Red-breasted Mergansers as this cannot be inferred from current mtDNA data.

Chapter 4 again addressed issues of site fidelity, genetic heterogeneity within nonbreeding groups, and the inherent bias of a single data type by investigating molt migration among male Common Mergansers on Kodiak Island, Alaska. In this chapter, I used mark-recapture data to assess recapture probability, mtDNA and morphological measures to infer population affiliation, and nuclear microsatellite genotypes to assess

the occurrence of two mechanisms that might contribute to genetic heterogeneity: seasonal migration and dispersal that results in gene flow. Using mtDNA haplotype baseline information from well-defined mtDNA haplogroups across North America, I was able to assign individuals to natal regions and document population genetic heterogeneity within and among molting groups. Band-recovery and DNA data suggested that both seasonal migration and dispersal contributed to admixed groups of males molting on Kodiak Island. This chapter also included an analysis of genetic differentiation across North America for nuclear DNA and found that male-mediated gene flow is likely very common. This suggested that natal area assignments of nonbreeding male Common Mergansers based on mtDNA may be uninformative as male dispersal leads to admixture on breeding as well as molting areas. These results have important implications for inferring levels of migratory connectivity (*sensu* Webster et al. 2002), especially for species with sex-biased dispersal such as the Common Merganser. In such cases, multiple and independent data types are required to account for such behaviors before accurate assessments of migratory connectivity can be made.

Overall, results from this dissertation provide information for four realms of biological science: the natural history of merganser species, the measurement and interpretation of site fidelity, population composition of breeding and nonbreeding groups, and the use of multiple data types to infer population structure. With regard to the natural history of merganser species, research presented in this dissertation offers new data for these information needs by summarizing patterns of migration, dispersal,

and gene flow from multiple data types across North America. While trend data suggest that all species of merganser are stable, if not increasing in North America, our understanding of population trends and general ecology of these species remains limited (Dugger et al. 1994, Titman 1999, Mallory and Metz 1999). This lack of basic biological information for mergansers has prompted the Sea Duck Joint Venture Management Board (2001) to list "Population Delineation" as the highest priority for Hooded Mergansers and "Population Dynamics" as the highest priority and most urgent information need for the management of Common and Red-breasted mergansers.

By comparing across the data generated for the three species examined here, I can offer some speculation on life-history strategies that each species has adopted, especially when viewed with some other recent information on merganser vital rates. Survival rates for adult female Hooded Mergansers (0.72; Chapter 2), Common Mergansers (range 0.42–0.82; Pearce et al. 2005), and Red-breasted Mergansers (0.64; Titman and Pearce, unpubl. data) average lower than other sea ducks, which typically exceed 90% (Krementz et al. 1997). Thus, mean annual survival rates of mergansers appear more similar to *r*-selected species (greater reproductive effort and lower survival), than to *K*-selected species (lower reproductive effort and higher survival). That is, life history traits of merganser species, such as larger clutch sizes (8–12) and lower survival rates, are more characteristic of species with higher reproductive effort and shorter life span than the sea duck group, which typically invests less in reproduction (smaller clutch size) and demonstrates higher survival and longer life spans. A prediction that warrants further examination is that cavity nesting sea ducks

incur a lower survival rate not because of body mass, as examined by Krementz et al. (1997), but because of higher reproductive effort. This prediction arises from the work of Geffen and Yom-Tov (2001) which found that clutch sizes are consistently larger among waterfowl species that nest in cavities, even after controlling for body mass and phylogeny. The Red-breasted Merganser appears to have retained the large clutch size trait, common among other cavity nesting sea ducks, even though it nests on the ground. A multi-locus sea duck phylogeny with life history characters mapped onto the tree is also needed in the near future to help evaluate not only the taxonomic evolution of the group, but the evolution of reproductive traits as well. Two final questions that also deserve some thought and future examination relate to dispersal and nesting habits of Hooded and Common Mergansers. If female dispersal occurs, as is suggested by data in Chapter 2, why is this species a rare breeder throughout Alaska and sympatric with other cavity nesting sea ducks? Forage for adults and young may be a limiting factor if habitat preferences are markedly different than species such as the Bufflehead (*Bucephala albeola*) and Common Goldeneye (*B. clangula*), which are common in Alaska and sympatric with Hooded Mergansers in more southerly locales. Secondly, why are Common Merganser females philopatric? What are the disadvantages to dispersal? Certainly, additional research on the nesting and brood rearing ecology of this species is needed, but studying natural cavity abundance and use is very challenging (Pearce, unpubl. data).

Data generated in Chapters 2, 3 and 4 all suggest that potentially different kinds of populations exist not only for each merganser species, but also within each species,

and these vary by age, sex, and time of year. Others may also exist. For example, I sampled adult female Hooded Mergansers in Chapter 2 to infer the population genetic signature of high site fidelity as inferred by mark-recapture data. Half of the females used in the mark-recapture analysis were known to have hatched locally, but the other half are of unknown origin. If this latter group of adult females dispersed to Mingo Swamp from other genetically divergent areas and then established site faithful behaviors to Mingo, then half of the DNA samples collected were from immigrants. Additionally, if adult females occasionally emigrate to other breeding areas to avoid nest site competition or perhaps to avoid a previous unsuccessful nesting attempt, then genetic attributes may be spread randomly across the landscape and over time, generate the inconsistent pattern of mtDNA I observed. Thus, multiple types of female breeding populations may exist in the Hooded Merganser.

For the Red-breasted Merganser, additional information is needed from non-genetic markers to evaluate site fidelity, migratory connectivity, and the possibility of more recent population structure than can be detected via mtDNA. Among Common Mergansers, there appear to be at least three types of population groups: (1) breeding females that are genetically differentiated across North America, and likely at even smaller scales, (2) a panmictic male population, and (3) heterogeneous populations of males and females during nonbreeding periods. I found little evidence for female gene flow among breeding areas. Thus, female breeding populations are the only groups that might be considered as management units based on genetic criteria (Moritz 1994).

As stated in Chapter 4, I do not conclude that low site fidelity results in heterogeneity within molting flocks of Common Mergansers, but instead view the two behaviors as decoupled. Site fidelity may or may not be advantageous because of species-specific traits related to foraging, survival, and reproduction. Thus, site fidelity and population structure should be kept as separate issues until sufficient data can be gathered to evaluate the two as somehow linked. There are examples in the literature of site faithful groups that are composed of multiple breeding populations (Bollinger and Derksen 1996, Dau et al. 2000), just as I have demonstrated that multiple breeding populations likely contribute to groups that show little if any site fidelity (Chapter 4).

Finally, the linkage of multiple markers, such as banding and genetic data, is important because both historical and contemporary factors influence the distribution and genetic differentiation of populations. While this idea is not new (see Avise et al. 1992), it has not been routinely applied, and more and more cases are finding that by combining data types, incorrect conclusions are being avoided had only a single marker type been used (see Arsenault et al. 2005, Fedy et al. 2008). Thus, the combination of these different markers allowed more confident conclusions about the location of population mixing and a possible mechanism for genetic similarity across the arctic. Since many arctic dwelling species have only recently colonized deglaciated areas, genetic similarity could mean that fidelity takes place, but is not manifested in genetic data. Therefore, direct estimates from banding and telemetry data are crucial to fully understand population movements in relation to genetic patterns.

The influence of site fidelity on population structure, especially during nonbreeding periods for species that pair during winter, will likely continue to be debated. For these species, additional information is needed on juvenile dispersal patterns and patterns of migratory connectivity between breeding and wintering areas. Without such information, no real progress can be made on the debate of winter site fidelity as a determinant of population structure. Certainly, the broader condition of site fidelity may have implications for fitness, mate pairing, and population delineation, but future investigations of site fidelity should be pursued without automatically invoking the term "philopatry" and assuming that the genetic and demographic connotations of natal philopatry also apply.

Literature Cited

Anderson, M. G., J. M. Rhymer, and F. C. Rowher. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. *In* Ecology and Management of Breeding Waterfowl, pp. 365–395. (B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.

Arsenault, D. P., P. B. Stacey, and G. A. Hoelzer. 2005. Mark-recapture and DNA fingerprinting data reveal high breeding-site fidelity, low natal philopatry, and low levels of genetic population differentiation in Flammulated Owls (*Otus flammeolus*). Auk 122:329–337.

Avise, J. C., R. T. Alisauskas, W. S. Nelson, and C. D. Ankney. 1992. Matriarchal population genetic structure in an avian species with female natal philopatry. Evolution 46:1084–1096.

Blums, P., J. D. Nichols, J. E. Hines, and A. Mednis. 2002. Sources of variation in survival and breeding site fidelity in three species of European ducks. Journal of Animal Ecology 71:438–450.

Bollinger, K. S., and D. V. Derksen. 1996. Demographic characteristics of molting Black Brant at Teshekpuk Lake, Alaska. Journal of Field Ornithology 67:141–158.

Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. *In* Marked Individuals in the Study of Bird Populations, pp. 199–213. (J.-D. Lebreton, and P. M. North, Eds.). Birkhauser Verlag, Basel, Switzerland.

Dau, C. P., P. L. Flint, and M. R. Petersen. 2000. Distribution of recoveries of Steller's eiders banded on the lower Alaska Peninsula, Alaska. Journal of Field Ornithology 71:541–548.

Doherty, P. F., Jr., J. D. Nichols, J. Tautin, J. F. Voelzer, G. W. Smith, D. S. Benning, V. R. Bentley, J. K. Bidwell, K. S. Bollinger, A. R. Brazda, E. K. Buelna, J. R. Goldsberry, R. J. King, F. H. Roetker, J. W. Solberg, P. P. Thorpe, and J. S. Wortham. 2002. Sources of variation in breeding-ground fidelity of Mallards (*Anas platyrhynchos*). Behavioral Ecology 13:543–550.

Dugger, B. D., K. M. Dugger, and L. H. Fredrickson. 1994. Hooded Merganser (*Lophodytes cucullatus*). *In* The Birds of North America, No. 98 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Dugger, K. M., B. D. Dugger, and L. H. Fredrickson. 1999. Annual survival rates of female Hooded Mergansers and Wood Ducks in southeastern Missouri. Wilson Bulletin 111:1–6.

Fedy, B. C., K. Martin, C. Ritland, and J. Young. 2008. Genetic and ecological data provide incongruent interpretation of population structure and dispersal in naturally subdivided populations of White-tailed Ptarmigan (*Lagopus leucura*). Molecular Ecology 17:1905–1917.

Geffen, E., and Y. Yom-Tov. 2001. Factors affecting the rates of intraspecific nest parasitism among Anseriformes and Galliformes. Animal Behavior 62:1027–1038.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and animals. Animal Behavior 28:1140–1162.

Iverson, S. A., D. Esler, and D. J. Rizzolo. 2004. Winter philopatry of Harlequin Ducks in Prince William Sound, Alaska. Condor 106:711–715.

Krementz, D. G., R. J. Barker, and J. D. Nichols. 1997. Sources of variation in waterfowl survival rates. Auk 114:93–102.

Lindberg, M. S., J. S. Sedinger, D. V. Derksen, and R. F. Rockwell. 1998. Natal and breeding philopatry in a Black Brant, *Branta bernicla nigricans*, metapopulation. Ecology 79:1893–1904.

Mallory, M., and K. Metz. 1999. Common Merganser (*Mergus merganser*). *In* The Birds of North America, No. 442 (A. Poole and F. Gill, Eds). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Mayr, E. 1963. Animal Species and Evolution. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Mehl, K. R., R. T. Alisauskas, K. A. Hobson, and D. K. Kellett. 2004. To winter east or west? Heterogeneity in winter philopatry in a central-arctic population of King Eiders. Condor 106:241–251.

Merom, K., Y. Yom-Tov, and R. McClery. 2000. Philopatry to stopover site and body condition of transient Reed Warblers during autumn migration through Israel. Condor 102:441–444.

Moritz, C. 1994. Defining 'evolutionary significant units' for conservation. Trends in Ecology and Evolution 9:373–75.

Pearce, J. M. 2007. Philopatry: A return to origins. Auk 124:1085–1087.

Pearce, J. M., J. A. Reed, and P. L. Flint. 2005. Geographic variation in survival and migratory tendency among North American Common Mergansers. Journal of Field Ornithology 76:109–216.

Robertson, G. J., and F. Cooke. 1999. Winter philopatry in waterfowl. Auk 116:20–34.

Sea Duck Joint Venture Management Board. 2001. Sea Duck Joint Venture Strategic Plan: 2001–2006. SDJV Continental Technical Team. Unpublished Report.

Shields, W. M. 1982. Philopatry, Inbreeding, and the Evolution of Sex. State University of New York Press, Albany, New York.

Svenning, M. A., R. Borgstrom, T. O. Dehli, G. Moen, R. T. Barrett, T. Pedersen, and W. Vader. 2005. The impact of marine fish predation on Atlantic salmon smolts (*Salmo salar*) in the Tana estuary, North Norway, in the presence of an alternative prey, lesser sandeel (*Ammodytes marinus*). Fisheries Research 76:466–474.

Titman, R. D. 1999. Red-breasted Merganser (*Mergus serrator*). *In* The birds of North America, No. 443 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Waples, R. S., and O. Gaggiotti. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Molecular Ecology 15:1419–1439.

Wells, J. V., and M. E. Richmond. 1995. Populations, meta-populations, and species populations: What are they and who should care? Wildlife Society Bulletin 23:458–462.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology and Evolution 17:76–83.

Wiese, F. K., J. K. Parrish, C. T. Thompson, and C. Maranto. 2008. Ecosystem-based management of predator-prey relationships: piscivorous birds and salmonids. Ecological Applications 18:681–700.

Wood, C. C., and C. M. Hand. 1985. Food-searching behavior of the Common Merganser (*Mergus merganser*) I: Functional responses to prey and predator density. Canadian Journal of Zoology 63:1260–1270.